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PART I. NATURAL SCIENCE

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II. *Social Science*

III. *Philosophy, Literature, and Art*

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Editor

SHERIDAN BAKER

PART I. NATURAL SCIENCE

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CONTENTS

Part I. Natural Science

GEOLOGY

The Transportation and Deposition of Chalcophile Metals by Sulfide and Polysulfide Complexes in Hydrothermal Solutions. Paul L. Cloke 5
The Solubility of Gold in Near-Surface Environments. William C. Kelly and Paul L. Cloke 19
New Exogyras from the Indidura Formation, Mexico. Lewis B. Kellum and Kenneth A. Shubak 31

PALEONTOLOGY

Upper Pliocene Geology and Vertebrate Paleontology of Part of the Meade Basin, Kansas. Michael O. Woodburne 61
A Late Pleistocene Molluscan Faunule from Meade County, Kansas. Barry B. Miller 103
The Mammals of the Cudahy Fauna. Gerald R. Paulson 127

BOTANY

Fossil Pollen Associated with a Late-Glacial Woodland Musk Ox in Michigan. William S. Benninghoff and Claude W. Hibbard 155
An Analysis of Streptomycete Populations in Soils. K. L. Jones. 161
A Peculiar Isolate of Allomyces. Frederick K. Sparrow and Barbara M. Morrison 175
Observations on Chytridiaceous Parasites of Phanerogams. X. Notes on Some Species of Physoderma Occurring in the Douglas Lake Region of Northern Michigan. Frederick K. Sparrow 183
Brevilegniella keratinophila gen. nov., sp. nov. M. W. Dick 195
Southern and Tropical Polypores, II. Josiah L. Lowe 205
Notes on Western Polypores. Robert L. Gilbertson 209

FORESTRY

Jack Pine Geographic Variation—Five-Year Results from Lower Michigan Tests. John L. Arend, Norman F. Smith, Stephen H. Spurr, and Jonathan W. Wright 219
Temperatures Near the Ground During Prescribed Burning. Robert E. Martin and Lawrence S. Davis 239
Crown Temperatures During Prescribed Burning in Jack Pine. William R. Beaufait 251
Some Observations on a Virgin Stand of Eastern White Pine. Eric A. Bourdo 259
The Effects of Stocking Level Cuttings on the Volume and Value of Residual Timber in a Northern Hardwood Stand. Thomas W. Church, Jr. 267

WILDLIFE

Winter Deer Mortality on Two Private Hunting Clubs. Ralph I. Blouch 277
Validity of Age Determination in Michigan Deer. Lawrence A. Ryel, Lawrence D. Fay, and Robert C. Van Etten 289

FISHERIES

Seasonal Mortality and Growth of Hatchery-Reared Brook and Rainbow Trout in East Fish Lake, Montmorency County, Michigan, 1958–59. G. R. Alexander and D. S. Shetter 317

ZOOLOGY

Late Cenozoic Cyprinid Fishes from Idaho, with Notes on Other Fossil Minnows in North America. Teruya Uyeno 329
Evolution of the Dorsal-Fin Supports of Percoid Fishes. C. Lavett Smith and Reeve M. Bailey 345
Man and the Changing Fish Fauna of the American Southwest. Robert Rush Miller 365
The North American Sciomyzidae Related to *Pherbellia fuscipes*. George Steyskal 405

PART I

NATURAL SCIENCE

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLVI, 1961 (1960 Meeting)

GEOLOGY

THE TRANSPORTATION AND DEPOSITION OF CHALCOPHILE METALS BY SULFIDE AND POLYSULFIDE COMPLEXES IN HYDROTHERMAL SOLUTIONS

Paul L. Cloke

The University of Michigan

Introduction

For many years speculations have been made concerning the manner of transport and deposition of sulfides in vein deposits. The geologic evidence indicates that the depositing medium contained water, the metal sulfides, and various gangue minerals. The most direct approach is to postulate that water, which is known to be present from its occurrence in the associated alteration minerals, is the solvent for these minerals. Most, if not all, of these minerals, however, are extremely insoluble in water, and this has cast doubt on the ability of water to act as the transporting medium. In spite of this it is assumed here that the ore-forming fluid is dominantly water, and an attempt will be made to show that under certain chemical conditions appreciable solubilities may be attained.

In recent years it has been suggested that the sulfides found in ore deposits may be carried in true solution as stable complexes containing both sulfur and metal. This paper considers the relations found experimentally for two such groups of complexes, namely, those with sulfides and those with polysulfides, and discusses the geologic implications of these relations.

The metal-sulfur complexes most likely to be of geologic importance are those that result from the combination of a compound of the metal or of a metal ion and a stable species of sulfur; i.e., a species which will not break down spontaneously into other sulfur species in the environment considered. A convenient summary of the stable sulfur species is provided by the Eh-pH diagram for sulfur in water.

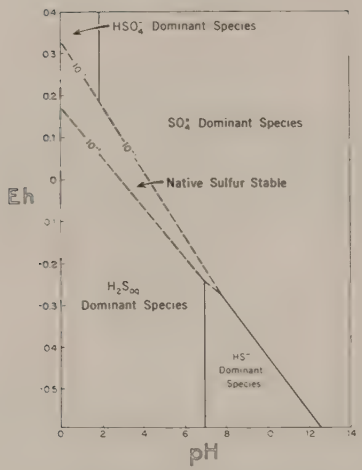

FIG. 1. The dependence of the distribution of sulfur species on pH and Eh at 1 atm. total pressure and 25° C. Alkalinity increases as pH increases; neutral is at pH 7. Oxidizing potential increases as Eh increases.

Such a diagram has recently been presented by Valensi (1951) and by Garrels and Naeser (1958). It is reproduced here as Fig. 1.

This diagram shows that at 25° C. and 1 atm. pressure the only stable sulfur species are those in which sulfur has a valence of −2, 0, or +6. The first consideration should, therefore, be directed to determining whether complexes with sulfides or sulfates are sufficiently stable to account for the solution and transportation of naturally occurring sulfides. It seems unlikely that "complexes" with elemental sulfur will be soluble in water.

Complexes with Sulfide Ion

A review of the chemical literature reveals that sulfides of at least 6 elements of interest dissolve with complex formation in sulfide solutions, but that no complexes with sulfate of sufficient stability are formed. Latimer and Hildebrand (1940) report that As_2S_3 (orpiment), Sb_2S_3 (stibnite), Sb_2S_4, and Sb_2S_5 are all soluble in excess sulfide ion at room temperature and pressure. As_2S_3 dissolves to form thioarsenite, AsS_3^{---}, which is easily oxidized by polysulfide to thioarsenate, AsS_4^{---}. As_2S_5 dissolves with excess sulfide ion to form

thioarsenate directly. In a similar way stibnite, Sb_2S_3, dissolves to form thioantimonite, SbS_3^{---}, which is oxidized by polysulfide to thioantimonate, SbS_4^{---}. Sb_2S_5 dissolves to form thioantimonate. Sb_2S_4 dissolves to form a mixture of thioantimonite and thioantimonate. Sidgwick (1950) reports that bismuthinite, Bi_2S_3, dissolves slowly in alkaline sulfide solutions. According to Latimer and Hildebrand (1940) stannic sulfide, SnS_2, is soluble in excess sulfide ion forming thiostannate, SnS_3^{--}, but SnS is not dissolved unless polysulfide is added, when it is oxidized to the soluble thiostannate. Dickson and Tunell (1955) have made an extensive study of the solubility of HgS (cinnabar and metacinnabar) in alkaline sulfide solutions and confirm the findings of Knox (1908) that the complex HgS_2^{--} is formed. They state that HgS is insoluble in polysulfide solutions, but give no details of the experiments. Gold dissolves to a limited extent as the complex AuS^- near the HS^--$SO_4^=$ boundary and close to neutral (cf. Garrels, 1960, p. 190).

All of these elements with the probable exception of tin are found in deposits formed at shallow depth and probably at moderate to low temperatures. The deposition of tin appears to be complicated by the reaction of the dissolved tin species (SnS_3^{--}?) and water to form SnO_2, cassiterite. The occurrence of realgar, orpiment, stibnite, bismuthinite, and gold in typical epithermal deposits is well known. Most of these elements are also found in deposits formed at greater depths and higher temperatures, but it is suggested that their mobility at low temperatures is related to the formation of sulfide complexes in which the average valence of sulfur is -2.

The effect of polysulfide on the solubility of SnS and also its ability to oxidize thioarsenite and thioantimonite suggest that the solubility of all of these compounds changes with Eh. Since the concentration of sulfide ion depends on pH, there must also be a change of solubility with pH. So far as I know, however, no study of the solubilities under controlled and measured conditions of both Eh and pH has been made.

Complexes with Other Metals

If copper, silver, lead, zinc, iron, and other metals are to be carried in a complex containing both sulfur and metal, it is necessary to postulate that the sulfur is in some valence state intermediate between -2 and $+6$, or that at higher temperatures and pressures

complexes with sulfide and/or sulfate occur that are unknown at room temperature. Only the former possibility will be considered here.

Probably the intermediate valence states of greatest geologic importance are those which are least unstable with respect to disproportionation into sulfide and sulfate. This restricts the consideration to complexes of thiosulfate, $S_2O_3^=$, and of polysulfide, $S_x^=$. Polysulfide may be formed by the reaction of sulfide ion and sulfur; e.g., $S^= + 3S = S_4^=$. Both of these come closest to attaining dominance as the principal sulfur species along the lines separating the fields of sulfate and sulfide species in Fig. 1. It is of interest to note that Barton (1957) and Natarajan (1958) have deduced in completely independent ways that this is exactly the region where ore transport is most likely.

The possibilities of complex formation with thiosulfates have been noted, but only the polysulfide complexes will be discussed.

Polysulfide Complexes

General.—Apparently very little detailed work has been done to determine the solubility of many of the sulfides in polysulfide solutions and little attention directed toward the influence of variable sulfur content on the solubility. It is generally recognized that the sulfides of manganese, iron, cobalt, nickel, copper, zinc, silver, lead, and a few other less common metals are essentially insoluble in "yellow ammonium sulfide." (As usually prepared this "yellow ammonium sulfide" has a $\bar{y}$ close to 2.)

$\bar{y}$ is defined as the ratio

$$\frac{\sum_{x=1}^{\infty} x\{[H_2S_x] + [HS_x^-] + [S_x^{--}]\}}{\sum_{x=1}^{\infty} \{[H_2S_x] + [HS_x^-] + [S_x^{--}]\}},$$

where the square brackets refer to the concentrations.

Copper.—In 1935 Höltje and Beckert measured the solubility of covellite, CuS, in polysulfide solutions at various sulfur contents and at various concentrations and temperatures. Their results are reproduced in Figs. 2, 3, and 4. Fig. 2 shows the increase of solubility with increasing sulfur content; projection of these curves to solutions saturated in sulfur ($\bar{y} = 4.9$) gives about 0.4 gm. of copper per liter

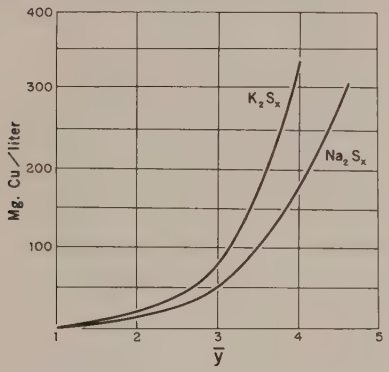

FIG. 2. Solubility of covellite, CuS, at 25° C. in polysulfide solutions containing 0.64 moles of K_2S_x or Na_2S_x per liter. $\bar{y}$ (defined on p. 8) increases as the dissolved sulfur content increases. (Höltje and Beckert, 1935)

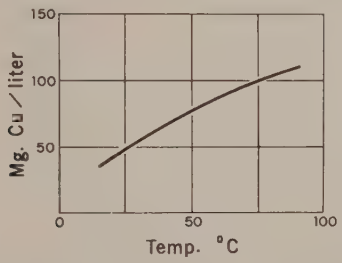

FIG. 3. Change of solubility of covellite with temperature in solutions containing 0.64 moles Na_2S_3/liter. (Höltje and Beckert, 1935)

for Na_2S_x solutions and 0.8 to 1.0 gm. of copper per liter for the K_2S_x solutions. Figure 3 shows the strong increase of solubility with rising temperature. If it is assumed that the solubility in solutions saturated in sulfur also doubles between 25° C. and 75° C. and that this rate of increase continues to 325° C., the solubility of CuS in Na_2S_x solutions can be estimated at nearly 3 gm. of copper per liter or about 0.05 moles/liter. As indicated by Garrels (1960) and Roedder (1959), concentrations far less than this are geologically significant. Fig. 4 shows the nearly linear change of solubility with concentration of Na_2S_3 .

Silver.—I have recently made a study of the solubility of silver

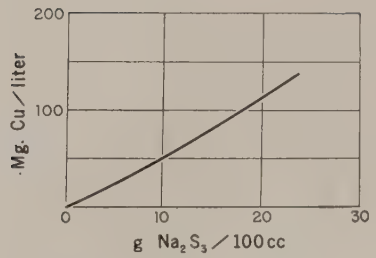

FIG. 4. Change of solubility of covellite at 25° C. with concentration of Na_2S_3. (Höltje and Beckert, 1935)

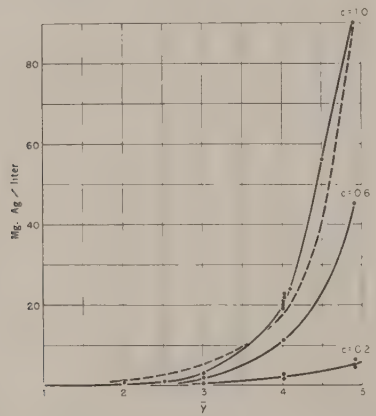

FIG. 5. Solubility of acanthite, Ag_2S, at 30° C. in polysulfide solutions. The solid lines show measured solubilities at three concentrations, designated in moles of sodium ion per liter by C. in the figure. The dashed line shows calculated solubilities for C. = 1.0 mole $Na^+/1$.

sulfide, Ag_2S, in sodium polysulfide solutions. The results are plotted in Figs. 5, 6, 7, and 8. Fig. 5 shows the effect of variable sulfur content and shows that silver behaves in the same way as copper. The maximum solubility is 90 mg. of silver per liter. Fig. 6 shows the effect of increasing temperature at two different values of $\bar{y}$. In both, the solubility is slightly more than doubled between 25° C. and 75° C. in remarkable conformity with the corresponding result for copper.

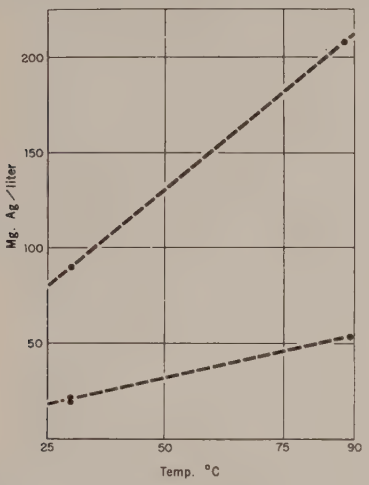

FIG. 6. Change of solubility of acanthite with temperature in solutions containing 1.0 moles $Na^+/1$. The upper line is for $\bar{y} = 4.9$ and the lower for $\bar{y} = 4.0$.

If the maximum solubility is projected to 325° C. in the same manner as for copper, a solubility a little over 0.5 gm. of silver per liter or about 5×10^{-3} moles per liter is obtained. Again this is a geologically significant concentration. The change of solubility with concentration is shown in Fig. 7 for three different values of $\bar{y}$; as might be expected the relations are nearly linear as with copper.

Geologic applications.—Before we can be reasonably sure that polysulfide complexes play an important role in ore deposition, solubilities must be determined and estimated under conditions of oxidation-reduction potential, acidity or alkalinity, temperature, and pressure which are geologically reasonable. In addition it seems likely that equilibrium or near equilibrium will be maintained; this implies that these geologically reasonable conditions must be such that the polysulfides will not completely disproportionate to sulfide and sulfate. A further restriction is that the sulfur content of the polysulfides be limited in some instances to low enough concentrations so that minerals low in sulfur as, for example, chalcocite, chalcopyrite, or

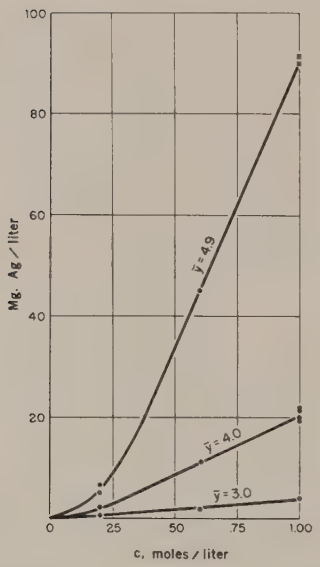

FIG. 7. Change of solubility of acanthite at 30° C. with concentration for $\bar{y}$ = 3.0, 4.0, and 4.9.

pyrrhotite, will not react to form minerals of higher sulfur content. Finally, the processes by which polysulfide solutions form, deposit metal sulfides, and disappear must be geologically feasible.

pH conditions.—It seems unlikely that solutions which are either strongly acid or strongly alkaline can persist in equilibrium with most rocks. In contrast the studies with polysulfides have been made in strongly alkaline solutions. To overcome this difficulty the solubility of silver sulfide was determined in sodium polysulfide solutions neutralized by hydrogen sulfide. The results are shown in Fig. 8 in which the experimental points are shown by solid circles and calculated solubilities by the lines. Details of the calculations will be presented in subsequent papers. One of the significant relations shown here is that the solubility in solutions saturated in sulfur drops only very slowly as the pH is lowered to 9, but then drops rapidly as pH is lowered to 7. At constant $\bar{y}$ the solubility drops with increasing alkalinity. The relations along the hydrolysis curve are the same as

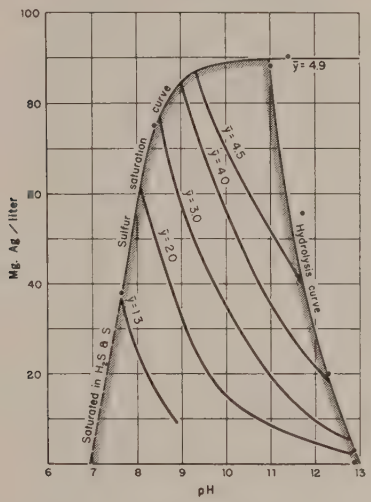

FIG. 8. Solubility of acanthite at various pH's and ȳ's at 30° C. The lines show calculated values and the points, measured values.

those shown in Fig. 5. The Eh of these slightly basic solutions is about −0.3 volt; this puts both Eh and pH into geologically reasonable ranges. This is also the region in which polysulfides have their maximum stability. In a very small part of this area the amount of sulfur contained in polysulfide at equilibrium equals that contained in hydrosulfide, HS^-, or in sulfate.

Thus it appears that solubilities are still significant for silver, and by analogy they should be for copper under equilibrium conditions that are geologically reasonable. The ranges of Eh and pH in which this is true, however, are extremely narrow at room temperature and pressure.

Temperature and pressure effects. —Studies at elevated temperatures and pressures in other systems have shown that such properties as solubilities and dissociation constants tend to vary linearly with increasing temperature if the density of the solutions is held constant by simultaneously increasing the pressure. The observed increases in solubility of CuS and Ag_2S with temperature tend to fit this pattern since the density of the solutions has not changed greatly in the intervals investigated.

Normally it would be expected that a decrease of pressure at constant temperature would cause a decrease of solubility, because the solution would become more like a gas, and solids are only slightly soluble in gases.

Application of these considerations is hindered by our uncertain knowledge of the pressure-temperature conditions during ore deposition. It is unlikely, however, that the pressure rises rapidly enough to keep the density constant as the temperature increases. There will, therefore, be a tendency to increase solubilities because of increasing temperature and at the same time to decrease them due to insufficient pressure increase. For the present it is assumed that the solubilities will stay the same or increase. Experiments are visualized to check this assumption.

Stability of polysulfides.—The region in which polysulfides may exist in appreciable amount at equilibrium at room temperature and pressure is extremely small. Unfortunately data are not available for determining whether this region increases in size at higher temperatures. This is a critical point, since if the size does not increase it seems unlikely that polysulfides contribute much to ore transport. For the present it will be assumed that the size of this region does increase as temperature rises, and attempts will be made to verify this experimentally.

Restrictions on sulfur content.—With polysulfide solutions containing very little dissolved sulfur, chalcocite and digenite will react at room temperature to form covellite. It is known, however, that at 507° C. (Kullerud, 1958) covellite breaks down to digenite and sulfur vapor. In other words at this temperature a polysulfide solution saturated in sulfur would not cause covellite to form. At intermediate temperatures, intermediate sulfur contents would mark the boundary between the digenite and covellite fields. Apparently, therefore, a high enough sulfur content to attain appreciable solubilities can be reached at elevated temperatures at a low enough sulfur content to allow chalcocite to be formed. By considering also the relations deduced by McKinstry and Kennedy (1957) it is seen that chalcopyrite and bornite would also be stable and (probably) appreciably soluble under these conditions.

Formation of polysulfide solutions.—These might be formed in various ways. Perhaps the best is to start with a source of sulfide

such as hydrogen sulfide. This H_2S would dissolve in water and react with adjacent rocks or magma and become neutral or slightly alkaline.

One way of producing polysulfide assumes that magnetite and hematite are present in the source area as accessories. Comparison of Fig. 1 with the Eh-pH diagram showing the magnetite-hematite boundary, as given by Garrels (1960), indicates that at room temperature and pressure the hematite-magnetite boundary lies slightly above the $HS^- - SO_4^{--}$ boundary in alkaline to slightly acid solutions. This means that hematite should oxidize hydrosulfide to sulfate. Once again data are lacking for higher temperatures, but it will be assumed that this relation also holds under the conditions in which ore solutions form. In these circumstances the H_2S -water solution will be slowly oxidized. Since it was previously assumed that the polysulfide field increases in size at higher temperatures, it follows that the first change results in the formation of a polysulfide solution.

A second way of producing polysulfide might be by oxidizing the sulfide by sulfur dioxide. Since SO_2 is present in volcanic gases, it seems possible that it may be present during the formation of hydrothermal solutions. This sulfur dioxide can then produce polysulfide according to a reaction such as,

$$5HS^- + SO_2 = 3S_2^= + 2H_2O + H^+.$$

This polysulfide solution can then dissolve copper and silver as well as barium and other elements from the source. Calculations based on estimated data given by Latimer (1952) indicate that arsenic, antimony, and tin are very soluble in the proper ranges of Eh and pH. Mercury and gold are only slightly soluble, but perhaps enough even at room temperature to be significant. It is anticipated that lead, zinc, and other elements found in ore deposits will also be found to be sufficiently soluble under these conditions.

Deposition from polysulfide solutions.—Once the polysulfide solution is formed there is no difficulty in visualizing ways to deposit ore minerals from it. Examination of Fig. 8 shows that increase of pH in the absence of elemental sulfur, such as by contact with limestone, will cause deposition. Decrease of pH would eventually cause deposition of sulfides and native sulfur. Examination of Fig. 1 shows that continued oxidation, such as by rocks containing hematite, would lead to the conversion of polysulfide to sulfate. This loss of polysulfide

would cause ore minerals to deposit, and the production of sulfate would lead to precipitation of such minerals as barite and alunite. Contact with carbonaceous beds, such as black shales, should lead to reduction of the polysulfide back to hydrosulfide, and again the loss of polysulfide would cause deposition.

Another interesting way of causing deposition is by pyritization of the wall rocks. Considering only the iron component of biotite, one can write

$$\underset{\text{(iron biotite)}}{KFe_3(AlSi_3O_{10})(OH)_2} + 3S_2^{--} + 2H_2O = \underset{\text{(pyrite)}}{3FeS_2} + \underset{\text{(orthoclase)}}{KAlSi_3O_8} + 6OH^-.$$

(The alteration of orthoclase in the walls is a separate problem and will not be considered here; the above reaction can easily be rewritten in terms of such alteration minerals as quartz and sericite or kaolinite with no effect on the conclusions drawn.) The result of this reaction is to remove polysulfide from the solution. This removal of polysulfide would in turn cause deposition of the ore minerals.

In agreement with the relations postulated previously, deposition should result from a drop of pressure or of temperature. In addition a drop of temperature should lead to a disproportionation of the polysulfide into hydrosulfide and sulfate, and thus to a disappearance of the ore solution.

Finally, a simple dilution should cause a small amount of deposition.

Zoning.—Some of the ways of depositing copper and silver from polysulfide solutions involve the removal or destruction of the polysulfide, but not of sulfide or hydrosulfide. If there should be any arsenic, antimony, bismuth, mercury, or gold in the solution initially, at least some should remain in solution as sulfide complexes. Movement of the solution toward the surface would then separate the remaining arsenic, antimony, etcetera, from copper and silver.

From the zoning found in ore deposits, it would be expected that lead and zinc are insoluble in sulfide solutions, but become soluble at lower sulfur contents than does copper. If so, the observed zoning is readily explained by a progressive loss of polysulfide from the postulated ore solution.

Summary

In conclusion the problem of ore transport and deposition has been considered in relation to the formation of sulfide and polysulfide complexes. Based upon geologically reasonable assumptions and known data it has been shown that metals, such as copper and silver, and presumably arsenic, antimony, mercury, gold, lead, and zinc, can be dissolved in polysulfide solutions. These solutions can be formed by geologically feasible processes, and would be expected to deposit ores in limestones, red beds, black shales, and iron-bearing rocks of all types. The occurrence of barite and alunite in the gangue is readily explained. Pyritization of the wall rocks seems to be best explained as a cause, not a result, of ore deposition. Finally, zoning of ore deposits appears as a natural result of the different types of complexes formed.

A number of points are still uncertain due to lack of data, but many of these points can be investigated experimentally. This work should lead to a better understanding of the geologic role of polysulfides.

The strong arguments in favor of this hypothesis are based on the large number of geologically observed relations that are explained in a straightforward manner.

LITERATURE CITED

Barton, P. B., Jr. 1957. Some Limitations on the Possible Composition of the Ore-Forming Fluid. Econ. Geol., 52: 333–353.

Dickson, F. W., and Tunell, G. 1955. Geochemical and Petrographic Aspects of Mercury Ore Deposits. Final Report, Office of Naval Research, Contract Nonr 233, Task Order 12, Project NR 081-174.

Garrels, R. M. 1960. Mineral Equilibria. Harper and Bros., New York. 254 pp.

—— and Naeser, C. R. 1958. Equilibrium Distribution of Dissolved Sulphur Species in Water at 25° C and 1 atm. Total Pressure. Geochimica et Cosmochimica Acta, 15: 113–130.

Höltje, R., and Beckert, J. 1935. Die Loslichkeit von Kupfersulfid in Alkalipolysulfidlösungen. Z. Anorg. Allgem. Chem., 222: 240–244.

Knox, J. 1908. A Study of the Sulphur Anion and of Complex Anions. Trans. Faraday Soc., 4: 29–48.

Kullerud, G. 1958. The Cu-S System. Carnegie Inst. of Wash. Year Book, 57: 215–218.

Latimer, W. M. 1952. The Oxidation States of the Elements and Their Potentials in Aqueous Solutions, 2nd ed. Prentice-Hall, Inc., New York, 392 pp.

—— AND HILDEBRAND, J. H. 1940. Reference Book of Inorganic Chemistry, rev. ed. Macmillan Co., New York, 563 pp.

MCKINSTRY, H. E., AND KENNEDY, G. C. 1957. Some Suggestions Concerning the Sequence of Certain Ore Minerals. Econ. Geol., 52: 379–390.

NATARAJAN, R. 1958. Personal communication.

ROEDDER, E. 1959. Fluid Inclusions as Samples of the Ore-Forming Fluids (Abstract). Geol. Soc. Amer. Bull., 70: 1663.

SIDGWICK, N. V. 1950. The Chemical Elements and Their Compounds. Vol. 1. Clarendon Press, Oxford, 853 pp.

VALENSI, G. 1951. Contribution au Diagramme Potential pH du Soufre. Proceedings, Second Meeting, Intern. Comm. Electrochemical Thermodynamics and Kinetics (CITCE). Libreria Editrice Politecnica Cesare Tamburini, Milan, 51–68.

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THE SOLUBILITY OF GOLD IN NEAR-SURFACE ENVIRONMENTS

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Introduction

In the past, there has been much speculation as to the chemical conditions under which gold will dissolve in near-surface geologic environments. As a rule, the metal is inert and tends to remain fixed as the more soluble materials are leached from an oxidizing ore deposit. Numerous exceptions have been cited, however, where the field evidence calls for extensive solution and transportation of gold; the unusual conditions leading to such exceptions are the subject of the present report.

In early studies of this problem Emmons (1917) pointed out that gold might be dissolved in acid solutions as the soluble auric chloride complex, provided a strong oxidizing agent such as manganese dioxide was present to convert gold to the auric state. Krauskopf (1951) has more recently considered the behavior of gold in the oxide zone as one phase of a more general study of the solubility of this element. He concluded that supergene transport of gold should take place in acid solutions in the presence of excess chloride ion and any one of a number of strong oxidizing agents, such as MnO_2, Fe^{+++}, Cu^{++}, or atmospheric oxygen. He also demonstrated that the driving force behind the manganese dioxide reaction is not, as formerly thought, the release of nascent chlorine gas. The function of the chloride ion is merely to combine with auric ion to form the soluble auric chloride complex.

The present study is to a large extent an expansion of Krauskopf's approach. Our purpose is to determine the theoretical ranges of acidity, oxidation potential, and chloride ion concentration within which gold should dissolve in geologically significant quantities. After a theoretical field of gold solubility is established, a comparison will be made between the calculated boundaries of this field and actual values of pH, Eh, and $(Cl^-)^*$ in mine waters.

* Parentheses indicate activity of the ion.

Criterion of Gold Solubility

In any study such as this it is necessary to accept some equilibrium activity of dissolved gold as a lower limit defining the geological solubility of the element. By a geologically soluble element, we mean one that gives definite evidence of extensive solution, transportation, and possibly redeposition within a short to moderate span of geologic time such as that required for oxidation of a sulfide ore body.

The selection of such a lower limit is at best an arbitrary decision based on the known solubilities of materials that are decidedly mobile or immobile in geologic environments. Therefore, the agreement that exists among competent geochemists as to cutoff values for geologic solubility is surprising. Garrels (1959, p. 118) has pointed out that activities of 10^{-1} or more for a given species indicate high geologic solubility. Indeed, at such high concentrations significant discrepancies between molalities and activities can be expected. At the other extreme, activities on the order of 10^{-8} moles liter or less indicate a negligible solubility. Garrels chooses a value of 10^{-6} as separating geologically mobile from immobile species.

In a study of the sedimentary controls of iron and manganese deposition, Krauskopf (1957, p. 65) uses an activity of 0.5 ppm. or approximately 10^{-5} moles liter as a limit for the solubility of iron and manganese minerals.

Another line of reasoning might be used in reaching a decision here. Roedder's recent studies (1959, p. 1663) of the chemical composition of fluid inclusions in transparent ore and gangue minerals of hydrothermal veins indicate that the concentration of metals in these fluids is only on the order of 0.1–1.0 ppm. For gold, this would correspond to a molality of 10^{-6} to 10^{-5}. If it is contended that these are true samples of the ore-forming fluids, and that such dilute solutions were actually responsible for deposition of an ore body within a short to moderate geologic time, then extensive leaching of metals from an ore body by supergene solutions of a comparable concentration is entirely within reason.

Based on these considerations, we have selected an equilibrium activity of about 2 ppm. or 10^{-5} moles per liter as the lower limit of gold solubility.

Stability of Dissolved Species in Equilibrium with Native Gold

The potentials relating the different oxidation states of gold are illustrated by the diagram in Fig. 1 (Latimer, 1952). Of the dissolved species shown here, only the auric ion and its soluble complexes are stable in aqueous solution. Aurous ion decomposes to form native gold and auric ion. Gold in the +2 state is also unstable in contact with water because it disproportionates to form the auric ion and native gold.

Acidity, oxidation potential, and chloride ion concentration are factors that delimit the stable dissolved species of gold in a particular

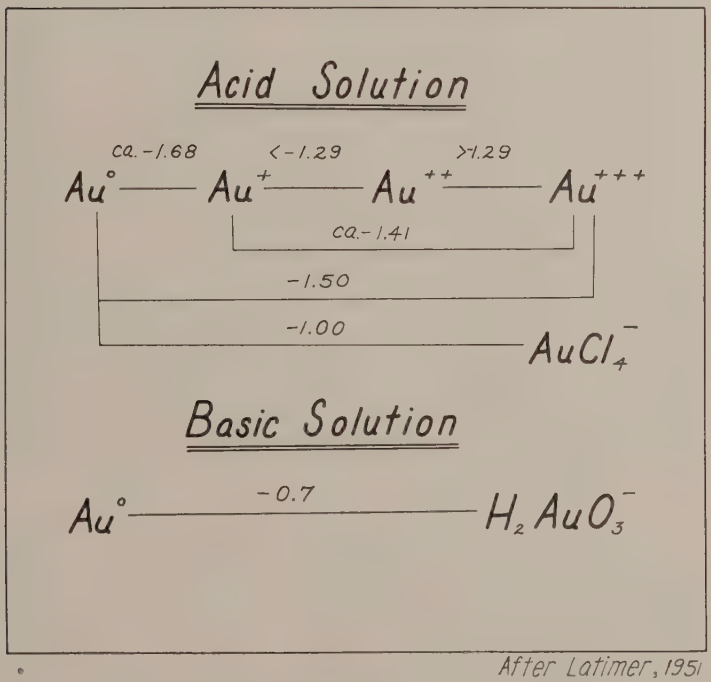

Fig. 1. Potential diagram for gold (Latimer, 1952).

TABLE I

Equilibria between Dissolved Gold Species

$3H_2O + Au^{+++} = H_2AuO_3^- + 4H^+$ (pH dependent)
$\Delta F^0 = 20.7$ Kcal., $K = 10^{-15.2}$
At equal activities of Au^{+++} and $H_2AuO_3^-$, pH = 3.8

$4Cl^- + Au^{+++} = AuCl_4^-$ (Cl^- dependent)
$\Delta F^0 = -34.4$ Kcal., $K = 10^{25.2}$
At equal activities of Au^{+++} and $AuCl_4^-$, $(Cl^-) = 10^{-6.3}$ M/1

$4H^+ + 4Cl^- + H_2AuO_3^- = AuCl_4^- + 3H_2O$ (pH, Cl^- dependent)
$\Delta F^0 = -55.1$ Kcal., $K = 10^{40.4}$

environment. The stability fields of Au^{---}, $H_2AuO_3^-$, and $AuCl_4^-$ may be calculated from thermodynamic data by conventional methods and these fields are shown in the isometric diagram in Fig. 2. The outer planes bounding the block in this diagram are governed by the ranges of pH, Eh, and (Cl^-) to be expected in nature. The limits of oxidation potential shown are those within which water itself is stable.

In acid solutions (pH less than 3.8) of low chloride content auric ion is the predominant gold species. In moderately acid to alkaline solutions with little chloride ion, the hydrated auric oxide complex predominates. In the presence of low to moderate amounts of chloride ion, both the auric ion and the oxide complex give way to the auric chloride complex. The reactions and equilibrium data relating these dissolved species are presented in Table I. At this point, it should be emphasized that these data only define which of the possible ions is dominant at equilibrium under the various conditions represented. They do not indicate the activity of dissolved gold in equilibrium with native gold.

Activities of Dissolved Species in Equilibrium with Native Gold

Knowing which of the dissolved auric species is dominant under given conditions of acidity, oxidation potential, and chloride ion concentration makes it possible to calculate the activity of this ion in equilibrium with native gold. Reactions and equilibrium data used in these calculations are given in Table II. A detailed explanation of the methods is given by Garrels (1959).

TABLE II

ACTIVITY OF DISSOLVED SPECIES IN EQUILIBRIUM WITH NATIVE GOLD

$$3H_2O + Au^0 = H_2AuO_3^- + 4H^+ + 3e^- \text{ (Eh, pH dependent)}$$
$$\Delta F^0 = 124.3 \text{ Kcal.}, E^0 = +1.80 \text{ volts}^*$$
$$E = 1.80 + .02 \log (H_2AuO_3^-) - .08 \log pH$$

$$4Cl^- + Au^0 = AuCl_4^- + 3e^- \text{ (Cl}^- \text{ dependent)}$$
$$\Delta F^0 = 69.2 \text{ Kcal.}, E^0 = +1.00 \text{ volts}$$
$$E = 1.00 + .02 \log (AuCl_4^-) - .08 \log (Cl^-)$$

$$Au^0 = Au^{+++} + 3e^- \text{ (Eh dependent)}$$
$$\Delta F^0 = 103.6 \text{ Kcal.}, E^0 = +1.50 \text{ volts}$$
$$E = 1.50 + .02 \log (Au^{+++})$$

* The sign convention of the American Electrochemical Society is used.

With this information, it is possible to contour the E_h-pH-(Cl^-) diagram shown in Fig. 2 with lines of equal dissolved gold activity, and such a modified diagram is shown in Fig. 3.

The general insolubility of gold is well illustrated here by the low activity values of contours covering most of the surface of this block. It is also evident that the maximum solution of gold should take place in the auric chloride complex field under conditions of high acidity, high oxidation potential, and high chloride ion concentration.

If, as previously discussed, an activity of 10^{-5} moles per liter is chosen as the criterion of gold solubility, then the field of gold solubility appears as a triangular wedge at pH values less than 5.5, Cl^- activities greater than $10^{-3.2}$, and oxidation potentials ranging from -0.90 up to the water stability boundary. Selection of a different lower limit of gold solubility such as 10^{-6} or 10^{-4} moles per liter would not change the shape or size of this field significantly.

ACIDITY, OXIDATION POTENTIAL, AND CHLORIDE ION CONCENTRATION OF ACTUAL MINE WATERS

The conditions under which gold should theoretically dissolve have been defined, but there remains the question of whether the required pH, Eh, and (Cl^-) ranges are actually attained in mine waters. This question is best answered by turning to actual measurements of these variables in mine waters, however few and inadequate these measurements may be.

Acidity and oxidation potential.—The factors of acidity and oxi-

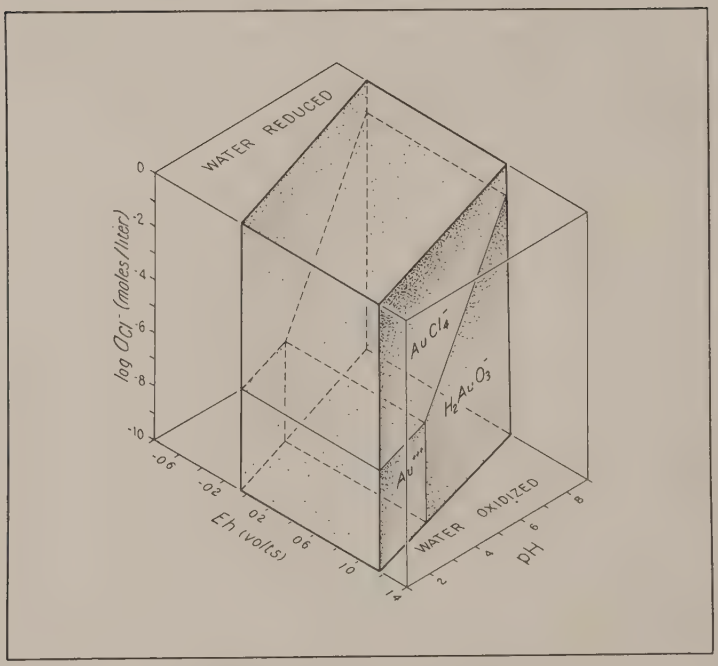

FIG. 2. Stability fields of dissolved auric species.

dation potential must be considered together since many oxidation-reduction reactions involve hydrogen ion, and the two factors are not independent in all cases. For the solution of gold, it is the combination of high E_h and low pH that is effective and not extreme values in one alone.

There is general agreement that the near-surface waters leaching an ore body are oxidizing and at times strongly acid. There are, however, very few published measurements of pH and E_h for mine waters. By simple recalculations of complete mine water analyses it is possible to group these waters into categories of primary acidity, primary alkalinity, and so on, but these groupings are semiquantitative and give no idea of the oxidation potential.

The only data of the type needed is that made available by Dr. Motoaki Sato (personal communication, 1960), who has measured

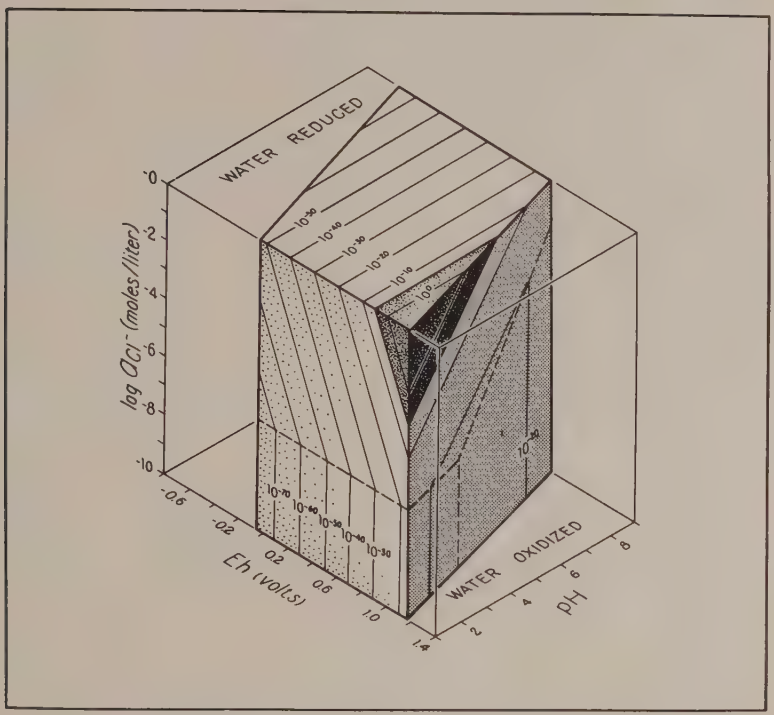

FIG. 3. Activities of ions in equilibrium with native gold.

the E_h and pH of some 44 natural mine waters. Seventeen of his measurements were made on waters of the oxide zone in sulfide ore deposits of western and southwestern states. Almost one half of the samples from oxide zones were sufficiently acid to dissolve gold, but none of Sato's measurements yielded E_h-pH combinations within the gold solubility field. Perhaps many additional such readings, especially in those mines where gold is purported to be mobile, would give values within the field, but the data at hand at least suggests the rarity of these conditions.

Of particular concern with reference to a problem such as the solubility of gold is the fact that certain mine waters in the oxide zone do not lend themselves to measurements of this kind. These are the very

first waters of a rain to reach and moisten dry oxide ground and, at the other extreme, the last moisture to survive evaporation and persist in oxide ground that has practically dried out. Such solutions probably contain abnormally high concentrations of soluble reagents that are diluted at times of maximum infiltration. There is little hope of measuring the E_h and pH of such waters because, by their very natures, the abnormal concentrations depend upon the absence of large measurable amounts of solvent.

Overvoltages may occur in natural solutions and would certainly favor the solution and transportation of gold. In this study, however, we have made the conservative assumption that the upper water boundary places a limit on natural potentials.

Chloride ion concentrations are better known than the other variables controlling gold solubility. Many analyses of mine waters have been published by Hodge (1915) and Emmons (1917). In Fig. 4, the

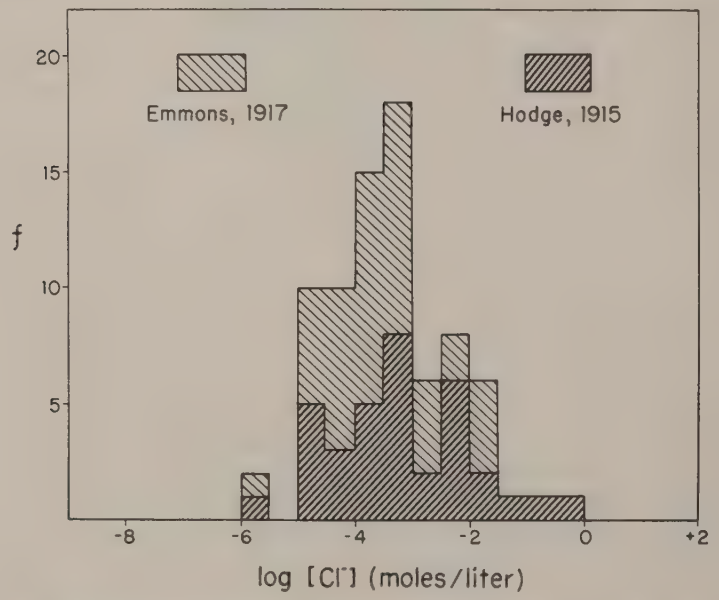

FIG. 4. Frequency distribution of chloride ion concentrations in 78 mine water samples.

frequency distribution of chloride ion data is shown for 78 of the analyses listed by these authors. It is evident from this distribution that the most frequent and also the majority of chloride ion concentrations fall at or below the minimum of $10^{-3.2}$ required for solution of gold. On the other hand, values between 10^{-3} and $10^{-1.5}$, well within the gold solubility field, are common.

Again, it should be stressed that these analyses do not represent the abnormal concentrations of near-surface solutions in ground that is practically dry.

Mechanisms for Oxidation of Gold

Several strong naturally occurring oxidizing agents have an appreciable effect on metallic gold in acid chloride solutions. Krauskopf (1951) has referred to manganese oxide, ferric ion, cupric ion, and atmospheric oxygen as being the most effective of these. Natural inorganic acids, in themselves, do not have sufficient oxidizing power to convert gold to the auric state.

It is of interest to specify the reactions of some of these oxidizing agents within the gold solubility field under the same conditions of acidity, oxidation potential, and chloride ion concentration. To date, we have studied the reactions of iron and manganese species since these are the most effective of possible oxidizing agents commonly associated with gold in the oxide zone.

Reactions of iron species.—Only goethite, FeO(OH), appears as a stable iron species within the gold solubility field. This is based on consideration of the free energies of formation of Fe^{++}, Fe^{+++}, $FeCl^{++}$, Fe_2O_3, $Fe(OH)_3$, and FeO(OH). Data for all except goethite are taken from Latimer (1952) and for goethite from Schmalz (1958).

The overall oxidation potential in surface mine waters is governed by the ratios of the activity of goethite to the stable reduced species—in this instance, the ratio of the activity of goethite to the activity of ferrous ion. These species are related by the following reaction:

$$2H_2O + Fe^{++} = FeO(OH) + 3H^+ + e^- \text{ (pH, Eh dependent)}$$

$$\Delta F^\circ = 16.7 \text{ Kcal., } E^\circ = +0.724 \text{ volts}$$

The oxidation potentials associated with this reaction may be calculated from the relationship:

$$E = 0.724 + .06 \log (FeO(OH)/Fe^{++}) - 0.18 \text{ pH}$$

Krauskopf (1951) has maintained that the solution of gold requires the absence of a strong reducing agent like ferrous ion. In the strict sense, however, it is the ratio of oxidized species to reduced species that governs the oxidation potential of the environment and not the absolute amount of reductant present. There will always be an activity for ferrous ion in this system even though it may be extremely small. In the present case the activities of ferrous ion are on the order of 10^{-5} to 10^{-7} moles per liter.

We are now in the process of estimating by laboratory experiment whether the oxidation potentials indicated by the gold diagrams are actually attained by the reagents involved. In one experiment ground goethite ($FeO \cdot OH$) was exposed to 0.1 molar HCl at an initial pH of 1.08. E_h and pH were recorded at frequent intervals. Steady values were attained after 24 hours at pH of 1.08 and an E_h of 1.135 volts well within the gold solubility zone.

Reactions of manganese species.—The reactions of manganese within the gold solubility field are slightly more complex. In this instance, two species predominate, manganese dioxide and manganous ion. The disposition of these stability fields is shown in the block diagram of Fig. 5. The wedge shape of this block is determined by the trace of the 10^{-5} activity line in Fig. 3.

The high potentials associated with reduction of manganese dioxide are governed by the reaction:

$$2H_2O + Mn^{++} = MnO_2 + 4H^+ + 2e^-$$

The potentials involved are given by the relation:

$$E = 1.23 + .03 \log (MnO_2)/(Mn^{++}) - .12 \text{ pH}$$

At $(MnO_2/(Mn^{++}) = 1$

$$E = 1.23 - .12 \text{ pH}$$

The ratios of activities of MnO_2 to Mn^{++} required for potentials high enough to oxidize gold to the +3 state are given in the E_h-pH diagram to the right of Fig. 5. The manganese chloride complex, $MnCl^{++}$, is not stable even at a one-molar chloride ion activity for which this diagram is drawn.

Two experiments have been made with manganese minerals. The first was with ground pyrolusite, MnO_2, and 0.1 molar HCl. The pH remained essentially constant at about 1.08 and the Eh rose to 1.18

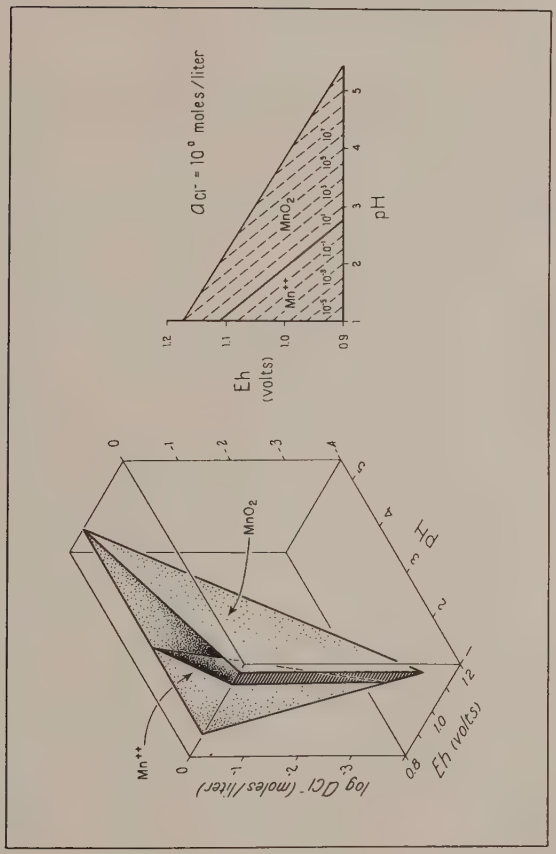

FIG. 5. Relations of manganese species within the gold solubility field.

volts after 63 hours. In the second ground manganite, $MnO(OH)$, was treated with 0.1 molar HCl for 51 hours. The final pH and Eh were 1.08 and 1.12 volts, respectively.

Summary and Conclusions

If an activity of 10^{-5} moles per liter is chosen as the lower limit of the geologic solubility of gold, the element is soluble in acid chloride solutions at pH values more acid than 5.5, oxidation potentials greater than 0.90 volts, and chloride ion activities over $10^{-3.2}$ moles per liter. The auric chloride complex is the stable dissolved species in this solubility field. The size or shape of the field is not changed appreciably by selection of 10^{-4} or 10^{-6} moles per liter as the cutoff for gold solubility.

Available data on actual mine waters indicate that the required chloride ion concentrations are fairly common. On the other hand, the combination of high acidity and high oxidation potential is more rare and may account for the general immobility of gold in the oxide zone.

Study of the equilibria of iron and manganese species within the gold solubility field indicates that the mechanisms for oxidation of gold to the auric state are the reductions of goethite, or limonite, to ferrous ion and the reduction of manganese dioxide to manganous ion. Preliminary tests indicate that the experimental potentials associated with these reactions compare closely with the calculated potentials.

LITERATURE CITED

Emmons, W. H. 1917. The Enrichment of Ore Deposits. U.S. Geological Surv. Bull. 625. 530 pp.

Garrels, R. M. 1959. Mineral Equilibria. New York: Harper and Bros. 254 pp.

Hodge, E. T. 1915. The Composition of Waters in Mines of Sulfide Ores. Econ. Geol., 10: 123–139.

Krauskopf, K. B. 1951. The Solubility of Gold. Econ. Geol., 48: 858–870.

—— 1957. Separation of Iron from Manganese in Sedimentary Processes. Geochimica et Cosmochimica Acta, 12: 61–84.

Latimer, W. M. 1952. Oxidation Potentials. Englewood Cliffs, N. J.: Prentice-Hall. 392 pp.

Roedder, E. 1959. Fluid Inclusions as Samples of the Ore-Forming Fluids (abstract). Geol. Soc. Amer. Bull., 70: 1663.

Schmalz, R. S. 1958. Thermodynamic Calculations Relating to the Origin of Red Beds (abstract). Geol. Soc. Amer. Bull., 69: 1639.

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Vol. XLVI, 1961 (1960 Meeting)

NEW EXOGYRAS FROM THE INDIDURA FORMATION, MEXICO

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Introduction

Determination of the stratigraphic position of a small collection of fossils from one locality near the western side of the Sierra de Tlahualilo in southwestern Coahuila is of unusual interest and importance because of its location on an outlying hill of limestone west of the main mountain front. We found no other fossils on similar outliers elsewhere along the west side of the range. This collection furnishes data necessary to determine the age of the rocks in the outlier and for the interpretation of structure at the margin of the range. The present investigation adds three new species of Exogyra to the fauna of the Indidura formation.

The authors recognize the limited value of naming new species of Ostreidae, but the occurrence of large and distinctive specimens not heretofore reported from the Indidura formation makes it seem useful to record their presence and morphological characters, in the hope that they may be found elsewhere and aid in correlation.

The fossil locality is some 30 miles north of the village of Tlahualilo de Zaragoza, Durango, which is about 40 miles north of Torreón, the industrial center of southern Coahuila (see inset on Fig. 1). An unimproved road from Tlahualilo extends northward along the valley west of the Sierra de Tlahualilo. The village of Tlahualilo was formerly owned by the Compañia Agricola, Industrial, Colonizadora, Limitada del Tlahualilo, S.A., which had its headquarters there. Most of the lands of the company were taken over by the Mexican Government in 1936 and its buildings sold. Gasoline and basic supplies can be purchased at the country stores and market in Tlahualilo or ordered to be sent from Torreón by truck, which makes the round trip to the city daily.

In 1953 University of Michigan geologists had a camp in the Cañon de Guayule about 2 miles east of the fossil locality designated

53-K-20. The senior author was assisted in the field by Robert M. Linsley, a graduate student, who collected some of the fossils.

The field work in 1953 was financed by grants made in November and December 1952 by the Executive Board of the Horace H. Rackham School of Graduate Studies of The University of Michigan and by the Executive Committee of the Michigan Memorial-Phoenix Project (Faculty Research Fund Project 874 and Michigan Memorial-Phoenix Project No. 62). This study is a contribution to a larger research program which was supported earlier by grants from the Geological Society of America and the Horace H. Rackham School of Graduate Studies (G.S.A. Project 386-41 and University of Michigan Research Project No. 115).

Previous Work

The fossils discussed in this report were discovered by the senior author in the course of planetable mapping in the Sierra de Tlahualilo. The only publication that refers specifically to the locality is one by him published in 1956. There (p. 207) it is included in a list of fossiliferous localities along the western side of the range. The number and location are followed in parentheses by this statement: "The fauna, mostly ostreidae, is not diagnostic of age." The location is on the map of fossil localities (Fig. 1) accompanying the report and its position shown with reference to the Arroyo Guayule and to two abandoned camps of migrant workers harvesting the wild candelilla and guayule plants in this arid region.

Elsewhere Kellum (1956, p. 208) says, speaking of the Aurora Limestone, "The fauna belongs to three distinct zones and to one locality, the stratigraphic position of which with reference to the others is not known." The one exception referred to is the locality 53-K-20, which yielded the fossils listed or described in the present report. Species listed from the locality 53-K-20 in table I of Kellum's 1956 report were: *Pecten indiduraensis* Jones, *Pecten* spp., *Nerinea?*, and *Kingena wacoensis* (Roemer). *Kingena wacoensis* occurs abundantly in the zone of *Gryphaea mucronata*, widely distributed in the Sierra de Tlahualilo, and has not previously been reported from the Indidura formation. *Pecten indiduraensis* is known only from the Indidura formation. Since the faunule of Collection 53-K-20 was predominantly made up of large exogyras not found in either the Aurora or the

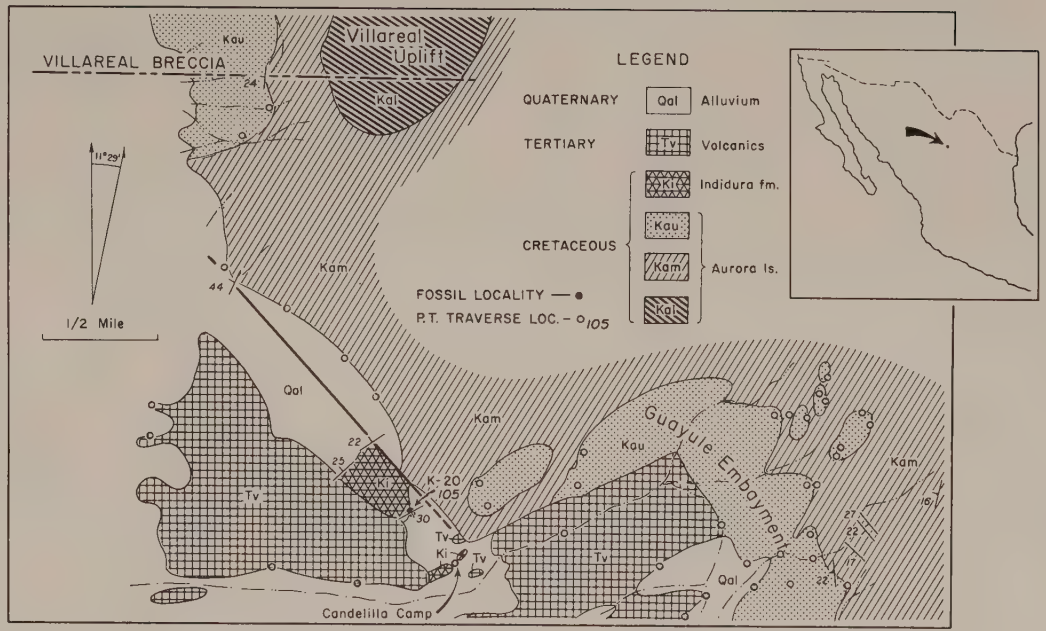


FIG. 1. Geologic map, south flank of the Villareal Uplift, Sierra de Tlahualilo, Durango, Mexico. By L. B. Kellum.

Indidura formations elsewhere in the Sierra de Tlahualilo, the author considered it to be undiagnostic.

The Indidura fauna, collected in other ranges of southern Coahuila, was described by T. S. Jones in 1938. He divided the formation into three members. The lowest, Member 1 of Middle and Upper Albian age, he correlates with formations in the north Texas section ranging from the Kiamichi formation of the upper Fredericksburg group, at the base to the Pawpaw formation of the middle Washita group at the top. Member 2 of Upper Albian, Cenomanian, and Lower Turonian age, he correlates with strata from the Main Street formation of the Washita group to the Lower Eagle Ford formation of the Gulf Series, including the Woodbine sand. Member 3, the highest, he correlates with the upper part of the Eagle Ford formation. Two species of Exogyra were reported: *E. plexa* Cragin from Member 1 and *E. arietina* Roemer var. *Coahuilaensis* Jones from Member 2.

Geologic Observations at Locality Where the Fossils Were Collected

Collection 53-K-20 was made at the southeast end of a small outlying area of limestone hills, about one quarter mile square, having a relief of some 50 feet. It is bordered on the southwest by a much larger area of volcanic deposits into which the limestone hills merge and on the other three sides by alluvium of the valley floor. That the limestone hills were formerly covered by volcanics is suggested by the fact that the contiguous volcanic hills rise to a higher elevation than the limestone hills.

The limestone is well stratified in beds varying up to several feet in thickness. At the northwest side of the outlying hills the beds on a dip slope strike northeast and dip at 25° to the northwest. The limestone is light gray with thin ferruginous layers and ferruginous nodules distributed irregularly in it. On the southeast side of the hills, where the fossils were found, the limestone is yellowish gray, hard and brittle. It weathers reddish and yellowish gray with exogyras projecting abundantly from its surface. The beds here strike northeast and dip at 30° to the southeast. The dip in opposite directions on the two sides indicates that the limestone hills comprising this small outlier are anticlinal.

Fossils in these outlying hills were, with one exception, found only at the one locality on a low ridge at the southeast side. The

importance of the fossils in determining the age of the outlying limestone hills, and therefore for the interpretation of structure, was recognized and a careful search of every outcropping layer made. The only other fossil found was a single specimen of *Alectryonia* in a limestone layer on the east side of the same ridge, but evidently from a somewhat lower stratigraphic level.

The fossils of Collection 53-K-20 at planetable station 105 were weathering out of the limestone and scattered over the surface. The conspicuous element of the fauna was the large exogyras, most of which were fragments. Smaller exogyras were better preserved and more abundant but difficult to break out of the hard rock. Therefore most of the collection was made from the float on, and in the immediate vicinity of, the small outcrop of the fossiliferous layer. Besides the exogyras, only half a dozen other forms were found, and some of these were discovered later in the limestone matrix when the specimens were being studied under a microscope in the laboratory.

With the exception of the exogyras the specimens are poorly preserved. The two gastropods are fragmentary casts. The single brachiopod has the original shell material preserved but most of the pedical valve is missing. The fragments of *Pecten* have the shell badly weathered. The two specimens of *Inoceramus* are pieces of valves, one of which has the shell material deeply weathered and the other is a mold of the exterior. The three fragmentary specimens of *Plicatula* are single valves with the shell badly pitted by weathering. The ostreidae have the original shell material and are in a much better state of preservation. However, the poorly preserved specimens associated with the ostreidae proved to be the more important for determining the stratigraphic position of the assemblage.

Geologic Relations to the Villareal Uplift

The Villareal uplift is a dome on the western side of the Sierra de Tlahualilo anticline, about 28 miles north of the south end of the range (Fig. 1). The dome extends about six miles in its north-south diameter, from the Gonzalez Basin on the north to the Guayule Embayment on the south. The gentler north flank is nearly twice as long as the south flank so that the apex is about 4 miles from the syncline on the north and 2 miles from the syncline on the south. On the east the Villareal Uplift merges with the major northward trending anticline of the range. Its western flank is cut by a normal fault which

begins here and extends northward along the front of the Sierra de Tlahualilo.

The surface expression of the uplift is developed principally in the middle member of the Aurora limestone, with a thickness of 1,040 feet along Cañón Guayule. The upper member, about 420 feet thick in the same section, is present in the synclines in three widely separated areas on the north, on the southeast, and on the west.

The outlier, from which the small collection of fossils described in this paper was derived, lies on the south flank of the Villareal Uplift. A fault separates it from the nearby outcrops of the Middle Aurora limestone. This outlier and several smaller limestone hills are somewhat farther isolated from the extensive outcrops of the Upper member of the Aurora exposed in the Guayule Embayment.

Lithologically the limestones of the outlier resemble some of those in the Upper Aurora member. Their geographic position on the south flank between areas of outcrop of the Upper Aurora on the southeast and on the west flanks of the Uplift suggest this stratigraphic correlation. The outlier had been so mapped until the fossils occurring there, described in the present report, proved to belong to the overlying Indidura formation. The Upper Aurora member is therefore absent from this part of the south flank. Evidently it has been dropped beneath the surface of the ground by the fault that separates the outlier from the main range. The fault that brings the Indidura formation down next to the middle member of the Aurora limestone therefore has a displacement of more than 400 feet.

A belt of Tertiary volcanics west and south of the limestone outlier forms low rugged hills connected with it. The volcanics are erosion remnants of a once widespread deposit of tuffs and lavas laid down on the eroded surfaces of Cretaceous rocks. Small patches of the volcanics are preserved today in the topographic and structural re-entrants of the western flank of the Sierra de Tlahualilo.

Correlation

The stratigraphic range of species related to those identified at locality 53-K-20 is shown in Table I and Fig. 2. They range from Upper Aptian to the Middle Turonian. Only one specimen, however, *Kingena wacoensis*, ranges as low as the Aptian. Three others, *Pecten indiduraense*, *Gryphaea washitaensis*, and *Plicatula subgurgitis*, range as low as the Middle Albian (Fredericksburg); they range as

TABLE I

GEOLOGIC RANGE OF FOSSILS RELATED TO SPECIES DETERMINED FROM LOCALITY 53-K-20

Species at Locality 53-K-20	Nearest Allied Species	Occurrence of Allied Species in Texas and Mexico
Kingena wacoensis (Roemer)	*K. wacoensis* (Roemer)	Common in Washita Division, rare in Fredericksburg and Trinity divisions in Texas. Widespread in *Gryphaea mucronata* zone in Sierra de Tlahualilo, Coahiula
Pecten indiduraensis Jones	*P. indiduraensis* Jones	Members 1, 2, & 3 of Indidura fm.
Gryphaea washitaensis Hill	*G. washitaensis* Hill	Kiamichi to Main St. fms. in Texas; Members 2 & 3 of Indidura fm.; Subdivisions 5 & 6 Cerro de Muleros, Chihuahua
Exogyra acroumbonata Kauffman	*E. acroumbonata* Kauffman	Graneros Shale (Colorado)
E. columbella Meek	*E. columbella* Meek	Woodbine and Eagle Ford
E. tlahualiloensis Kellum & Shubak	*E. clarki* Shattuck	Buda Ls. in Texas
E. extenda Kellum & Shubak	*E. suborbiculata* Lamarck, Stanton	*Pugnellus* SS. (Turonian)
E. robusta Kellum & Shubak	*E. whitneyi* Böse	Subdivisions 7 & 8, Cerro de Muleros Chih. (= Main Street and Grayson in Texas)
Plicatula subgurgitis Böse	*P. subgurgitis* Böse	Members 1, 2, & 3 Indidura Fm.; Subdivisions 2, 5, & 6, Middle & Upper Albian, Cerro de Muleros, Chihuahua Denton fm., Texas
Trigonarca sp. cf. *T. depressa* (White)	*T. depressa* (White)	Colorado fauna in N. M. *Pugnellus* Sandstone

high as the mid-Turonian (Eagle Ford). One species, *Exogyra whitneyi,* ranges from the Upper Albian into the Lower Cenomanian. Another, *Exogyra clarki,* is known only from the Buda Limestone (Lower Cenomanian). Two species, *Exogyra acroumbonata* and *Exogyra columbella,* range from the Cenomanian into the Turonian.

Fig. 2. Stratigraphic range of species collected at locality 53-K-20.

Two other species, *Trigonarca depressa* and *Exogyra suborbiculata,* are known only from the Turonian.

Since only four long-ranging species and one other of more limited known range extend below the Cenomanian, all the species range into the Cenomanian, two have a range from mid-Cenomanian into mid-Turonian, and two are limited to the mid-Turonian, the weight of the paleontologic evidence is that the fauna from locality 53-K-20 is of Cenomanian age. In the Sierra de Tlahualilo the upper part of the Aurora Limestone has been correlated (Kellum, 1956, p. 215) with the Georgetown limestone (Upper Albian) of Texas. The lower part of the overlying Indidura formation is at least as low as the Del Rio Clay (Lower Cenomanian) and its upper part as high as the Eagle Ford (Upper Cenomanian and Turonian) of Texas.

In the type area of the Indidura formation (Sierra de Santa Ana) it ranges from the Middle Albian to the top of the Turonian. Its middle member ranges from the Upper Albian through the Cenomanian and into the lower Turonian. The limestones which contain the fossils at locality 53-K-20 are therefore correlated with the middle member of the Indidura formation in the type area.

Habitat

In his study of the Indidura fauna of Sierra de Santa Ana and Sierra de la Peña Jones (1938) inferred, primarily on the basis of lithology, a moderately shallow marine environment for the rocks of Member 2. Conditions before and after deposition of Member 2 were characterized by quiet water; accumulation of calcareous mud and organic material rendered the sediments black in color.

The lithology of the strata at locality 53-K-20 is quite different from that of the Indidura formation in the type area. The absence of clastics indicates deposition in clear water. Some idea of the ecology may be obtained from an analysis of published data on the fossil and living genera related to the genera of our faunule. The genera *Ostrea, Gryphaea,* and *Exogyra* have long been considered valid criteria for shallow water deposition (Jourdy, 1924; Böse and Cavins, 1927, p. 48, 73; Imlay, 1957, p. 494; Bergquist and Cobban, 1957, pp. 872–871) and although commonly associated together *Gryphaea* and *Exogyra* are usually considered to inhabit more saline and deeper waters than the thick-shelled *Ostrea* (Bergquist and Cobban, 1957, p. 872). Jourdy concludes a shallow marine environment for *Exogyra*

with agitated waters and either muddy or sandy bottoms or near colonies of corals or rudistids. Stephenson (1933) believes the sediments of the *E. cancellata* belt, extending from the northern end of the Atlantic Coastal Plain to the Gulf region, were laid down on a continental shelf in water ranging in depth from 15 to less that 100 fathoms. Rudistids associated with the fauna are believed to indicate a tropical climate.

Individuals of *Gryphaea* and *Exogyra* collected at locality 53-K-20 occur for the most part as unpaired valves. However, a number of specimens are paired, and therefore transportation over any appreciable distance seems unlikely. Both genera are abundant and their association appears to be a natural one.

The genus *Trigonarca* is represented by only a single individual, but its presence is significant in the light of the work of Reinhart (1943) on the Mesozoic and Cenozoic Arcidae from the Pacific Slope of North America. Reinhart concludes that since most of the living *arcidae* are strictly marine, confined to tropical and temperate seas, inhabit the littoral and sublittoral zones and the shallower part of the neritic zone, the environment of the fossil arcidae could be expected to be similar. *Trigonarca* was the only representative of the family during the Cretaceous from Reinhart's collection.

Pecten is one of the few pelecypods that are found in rudistid reefs (Bergquist and Cobban, 1957). Matthews (1951) reports such an association of single valves in two rudistid reefs in the Lower Cretaceous Edwards limestone. It is assumed that the Pectens were washed into the reef after death. Deposition took place in warm, clear, shallow water (10–20 fathoms) of normal salinity.

It would seem probable then that the Indidura formation at locality 53-K-20 was deposited in warm, shallow (15–100 fathoms) marine water of normal salinity. The water was clear and therefore represents offshore conditions.

SYSTEMATIC PALEONTOLOGY

BRACHIAPODA

Genus KINGENA Davidson

Kingena wacoensis (Roemer)

(Pl. III, Fig. 1)

Diagnosis.—This species is represented in the collection by one highly weathered specimen.

Shell of medium size and average thickness, subcircular in outline, lenticular in profile; shell weathered, exposing punctations of inner layer; brachial valve has low convexity; most of pedicle valve missing.

Dimensions.—Length 20 mm., width 20 mm., thickness of brachial valve 4 mm.

Hypotype.—UMMP 33168.

Occurrence.—Common throughout the Washita division, and rare in the Fredericksburg and Trinity divisions in Texas; widespread in the *Gryphaea mucronata* zone in the Sierra de Tlahualilo.

PELECYPODA

Genus PLICATULA Lamarck

Plicatula subgurgitis Böse

(Pl. I, Fig. 16)

1910. *Plicatula subgurgitis* Böse, Inst. Geol. México, Bol. 25: 100, pl. 15, figs. 21–23.

1938. *P. subgurgitis* Böse. Jones, Geol. Soc. America Bull., 49 (1): 109, pl. 3, figs. 6, 7, 9, 11, 12.

Diagnosis.—Three fragmentary valves are in Collection 53-K-20.

Specimens badly weathered but show the bifurcating radiating costae. The growth lines, as noted by Böse (1910, p. 100), have developed irregular granulations of the costae and, in our specimens, weathering has further emphasized these, giving the costae a beaded character.

Dimensions.—UMMP 42324: length 7 mm., width 5 mm.

Catalogue number.—UMMP 42324.

Occurrence.—Denton formation, Texas; Cerro de Muleros, Chihuahua; Subdivisions 2, 5, 6, Middle and Upper Albian, Members 1, 2, 3, Indidura formation, Coahuila.

Genus INOCERAMUS Sowerby

Inoceramus spp.

(Pl. I, Fig. 14; Pl. III, Figs. 2, 4)

Description.—Two very small specimens and one fragment of a larger form, found at locality 53-K-20, clearly belong to three separate species.

UMMP 42323 is the mold of an interior. It is oval in outline, broadly rounded at the ventral margin, and tapering symmetrically to a narrowly rounded dorsal margin; beak elevated and bluntly pointed on mold. Dimensions: Length 8 mm., width 6 mm., height 1 mm.

UMMP 42322 is the cast of an exterior natural mold. It is rounded in outline; concentric undulations irregular, coarser toward the margins, faint toward the umbo; disk elevated near the umbo, flattening toward the margins. Dimensions: Length 3.2 mm., width 2.2 mm., height 0.6 mm.

UMMP 42327 is a small fragment of the cast, near the marginal area, of a fairly large specimen characterized by coarse undulations.

Genus EXOGYRA Say

Exogyra tlahualiloensis Kellum and Shubak n. sp.

(Pl. II, Figs. 2, 3; Pl. III, Fig. 8; Pl. IV, Figs. 1–3)

Description.—Based on four lower valves from locality 53-K-20.

Shell medium to large, ovate in outline, moderately thick in umbonal region, thinner at margins; steeply convex, subtriangular in transverse section (anterior-posterior at the middle of valve); beak conspicuously recurved; prominent angular umbonal ridge curving back from beak over middle of valve and disappearing on the ventral slope; surface covered with rough, lamellose growth lines, also a rugose area on the posterodorsal slope behind beak on the holotype. Interior smooth, deep; hinge narrow, ligamental groove moderately impressed, narrow groove below and posterior to ligamental groove expands to form broadly flattened free margin; semi-circular, impressed adductor scar on the steep posterior slope. Upper valve unknown.

Dimensions of Holotype 42297.—Length 102 mm., breadth 81 mm., convexity 45 mm.

Remarks.—This species differs from *Exogyra clarki* Shattuck in the absence of radial ribbing and its higher more prominent umbonal ridge. It differs from *Exogyra drakei* Cragin in its larger size, less strong concentric ornamentation, and absence of extensive radial plications.

Holotype.—UMMP 42297; Hypotypes 42303, 42304, 42305.

Exogyra acroumbonata Kauffman n. sp. in press

(Pl. I, Figs. 1, 2, 8, 9)

Diagnosis.—The description is based on one specimen from the Indidura formation, Sierra de Tlahualilo, Coahuila.

Shell small, thin, outline ovoid; lower valve triangular, beak narrow, laterally recurved, prominent umbonal ridge following spiral of shell from beak across middle of shell to posteroventral margin; posterodorsal part of shell concave, expanding ventrally and becoming convex; shell smooth except for growth lines. Upper valve not visible on our specimen.

Dimensions.—Length 5.5 mm., breadth 5 mm., convexity 2.5 mm.

Remarks.—The specimen agrees well with Kauffman's species aside from being slightly smaller. Kauffman's holotype is figured (Pl. I, Figs. 1, 8) for comparison.

Hypotype.—UMMP 42295.

Occurrence.—Indidura formation, Sierra de Tlahualilo, Coahuila; Graneros shale of the Western Interior.

Exogyra columbella Meek

(Pl. I, Figs. 3–7, 10–12, 22, 23)

1876. *Exogyra columbella* Meek, *in* Macomb, Rept. Expl. Exped. Santa Fe, N. Mex., to junction of Grand and Green rivers, p. 124, pl. 1, figs. 3a–d.

?1877. *E. costata* var. *fluminus* White, U.S. Geog. and Geol. Expl. Survs. W. 100th Mer. Rept., 4(1): 174, pl. 17, figs. 3a–d.
1884. *E. columbella* Meek. White, U.S. Geol. Surv. 4th Ann. Rept., p. 304, pl. 55, figs. 5, 6.
1893. *E. columbella* Meek. Cragin, Texas Geol. Surv. 4th Ann. Rept., 1892, p. 184.
1894. *E. columbella* Meek. Stanton, U.S. Geol. Surv. Bull., 106: 63, pl. 8, figs. 2–4.
1900. *E. columbella* Meek. Herrick and Johnson, Denison Univ., Sci. Lab. Bull., 11: 203.
1927. *E. columbella* Meek. Reagan, Indiana Acad. Sci. Proc., 36 (1926): 125, text figs. 3–7.
1928. *E. columbella* Meek. Adkins, Texas Univ. Bull., 2838: 115.
1951. *E. columbella* Meek. Adkins and Lozo, Fondren Science Series 4 (Dallas), pl. 3, fig. 1 (following p. 163).
1952. *E. columbella* Meek. Stephenson, U.S. Geol. Surv. Prof. Paper, 242: 77, pl. 17, figs. 4–6.

Diagnosis.—Six of these small exogyras were found at locality 53-K-20, Indidura formation, Sierra de Tlahualilo, Coahuila.

Shell small to medium, rather thin-shelled for the genus, outline subcircular with prominent beak; lower valve moderately to steeply convex, beak recurved in plane parallel to posterior slope; umbonal ridge broad and poorly developed; surface with fine costae radiating from the umbonal ridge, or smooth except for growth lines. Upper valve not visible on our specimens although some of the free flat valves may belong to this species.

Dimensions.—UMMP 42291, length 22 mm., breadth 19 mm., convexity 13 mm., UMMP 42292, length 18.5 mm., breadth 16 mm., convexity 9 mm., UMMP 42326, length 14.5 mm., breadth 13 mm., convexity 4.5 mm., UMMP 42294, length 12.5 mm., breadth 10.5 mm., convexity 6 mm.

Remarks.—The specimens from our locality resemble most closely the cotype figured by Meek (1876, pl. I, fig. 3a) showing well-developed costae and a rather prominent umbonal ridge of the lower valve. Our specimens are somewhat more convex than indicated by the side view figured by Meek (1876, pl. I, fig. 3c).

Hypotypes.—UMMP 42291–42294, 42301, 42302, 42311, 42325, 42326.

Occurrence.—Woodbine formation, Tarrant, Denton, Grayson, and Lamar counties, Texas; in Western Interior, beds of Graneros (Cenomanian) and Benton (Turonian) age; Indidura formation, Coahuila, Mexico.

Exogyra extenda Kellum and Shubak n. sp.

(Pl. I, Figs. 18–21, 24, 25, 27–29)

Description.—This is the most common species in our Collection 53-K-20.

Shell small to medium thin; subovate in outline; lower valve very convex, with broadly rounded umbonal ridge, extending from the beak to ventral margin. Some specimens are nearly symmetrical, sloping equally anteriorly and posteriorly from the umbonal ridge, others tend to be somewhat asymmetrical with the posterior slope steeper than the anterior. This variation may be emphasized by the state of preservation as the margins flare broadly, are thin, and are broken in most specimens. No posterior or anterior furrows present; beak

small, narrow, distinctly coiled posteriorly at tip; surface smooth except for growth lines, radial costae about umbo present in a few specimens.

Upper valve slightly smaller than lower, undulating, outline subovate, umbo small and spirally coiled; surface marked by fine rather regularly spaced growth lines.

Dimensions.—UMMP 42289, length 31 mm., breadth 32 mm., convexity 15 mm.; UMMP 42309, length 35 mm., breadth 38 mm., convexity 20 mm.; UMMP 42310, length 45 mm., breadth 40 mm., convexity 21 mm.

Remarks.—This species resembles both *Exogyra suborbiculata* Lamarck and *E. haarmanni* Böse but differs in position of rounded umbone. In *E. suborbiculata* and *E. haarmanni* the crest is nearer the anterior margin rather than the posterior as in ours. Our species also lacks the posterior furrow characteristic of *E. suborbiculata.*

Holotype.—UMMP 42290.

Hypotypes.—UMMP 36816, 36817, 42289, 42309, 42310.

Exogyra robusta Kellum and Shubak n. sp.

(Pl. II, Figs. 1, 4; Pl. III, Fig. 11)

Description.—Based on one lower valve from locality 53-K-20.

Shell large, massive, elongate ovate in outline, extremely thick-shelled but thinning somewhat toward margins so that at most places the margin is broken. Valve convex, broadly rounded with anterior and posterior slopes nearly vertical; beak recurved, coiling partially concealed by excessive deposition of shell material over it. Surface marked by thin-edged concentric imbrications; roughly radiating nodes on umbonal region may be the result of weathering; interior smooth and shallow. Upper valve unknown.

Dimensions of incomplete specimen.—Length 109 mm., breadth 67 mm., convexity 54 mm.

Remarks.—This species differs from *Exogyra whitneyi* Böse in the absence of an excavated area beneath the beak and its less prominent, more compactly recurved beak, and from *E. ferox* Cragin in its more shallow depth of the upper valve interior and in the lesser degree of beak coiling.

Holotype.—UMMP 42296.

Exogyra? sp.

(Pl. III, Fig. 3)

Description.—A fragment of a valve with an unusual structure and type of preservation seems worthy of record. It is part of the beak area of a large flat specimen, but the beak itself is missing.

Shell moderately thick, made up of thin layers varying in texture and color. Surface sculpture of deeply weathered concentric imbrications around an asymmetrical, U-shaped, channeled attachment scar. There are three layers of dense, light gray calcite alternating with thinly laminated, dark gray layers. The light gray layers, although dense, have a transverse fibrous structure on which the

surface sculpture is developed. One layer forms the outer surface of the shell near the attachment scar. Beyond it one of the inner layers of dense gray calcite becomes the outer surface as the intervening darker laminated layer lenses out. The imbrications of the surface sculpture are diagonally transverse to the inner surface of the layer and to the outer surface of the shell. The fibrous structure of the imbrications is perpendicular to their surfaces. In plan the concentric imbrications coalesce to form a smaller number as they approach the hinge line. The surface imbrications are of irregular relief and are pitted and furrowed by solution.

Hypotype.—UMMP 42329.

Genus GRYPHAEA Lamarck

Gryphaea washitaensis Hill

(Pl. V, Figs. 1–5, 8, 9)

1884. *Gryphaea pitcheri* White (part) (not Morton), U.S. Geol. Surv. Ann. Rept., 4: 302, pl. 49, figs. 1–2.
1898. *G. washitaensis* Hill. Hill and Vaughan, U.S. Geol. Surv. Bull., 151: 59, pl. 19, figs. 3–5, 7–19, pls. 19–22, pl. 23, figs. 1–3.
1901. *G. washitaensis* Hill. Hill, U.S. Geol. Surv. 21st Ann. Rept., pt. 7, pl. 36, fig. 3.
1906. *G. washitaensis* Hill. Veatch, U.S. Geol. Surv. Prof. Paper 46, pl. 7, fig. 2, 2a.
1910. *G. pitcheri* var. *washitaensis* Hill, Böse, Inst. Geol. México, Bol., 25: 110, pl. 20, figs. 1–13.
1920. *G. washitaensis* Hill. Adkins and Winton, Texas Univ. Bull., 1945: 62, pl. 15, figs. 5–12.
1925. *G. washitaensis* Hill. Winton, Texas Univ. Bull. 2544: 53, pl. 7, fig. 7.
1925. *G. washitaensis* Hill. Mahon, *in* Winton, Texas Univ. Bull., 2544: 68, pl. 24, fig. 7.
1927. *G. washitaensis* Hill. Bybee and Bullard, Texas Univ. Bull., 2710: 50, pl. 7, figs. 10, 11.
1928. *G. washitaensis* Hill. Adkins, Texas Univ. Bull., 2838: 107.
1938. *G. washitaensis* Hill. Jones, Geol. Soc. America Bull., 49(1): 107, pl. 3, figs. 14–16.
1947. *G. washitaensis* Hill. Stanton, U.S. Geol. Surv. Prof. Paper, 211: 29, pl. 16, figs. 1–4, 7–9.

Diagnosis.—Shell variable in size and shape, medium to small, thin to moderately robust; outline ovate; lower valve moderately convex, triangular wing on posterior margin present on some specimens, fragile and broken off of many specimens; usually separated from rest of shell by a shallow radial sulcus extending from near the beak to the posteroventral margin; beak broad and rounded, commonly obscured by flattened attachment scar; surface marked by fine to coarse concentric growth lines and lamellae; upper valve somewhat smaller than lower, circular in outline, flat but often depressed below umbo; surface marked by concentric growth lines.

Dimensions.—UMMP 42299, length 35.5 mm., breadth 32 mm., height 12 mm.; UMMP 42312, length 37 mm., breadth 33 mm., height 14.5 mm.; UMMP

42298, length 31 mm., breadth 30 mm., height 12.5 mm.; UMMP 42300, length 12 mm., breadth 11.5 mm., height 5.5 mm.

Hypotypes.—UMMP 42298–42300, 42312, 42343, 42344.

Occurrence.—Indidura formation, Coahuila; Cerro de Muleros, Chihuahua, Subdivisions 5 and 6, Upper Albian; Kiamichi to Main Street formations, Texas.

Remarks.—As stated by Hill and Vaughan (1898, p. 62) "This species presents an enormous amount of variation. In some the lateral wings are very much developed; in other specimens they are but slightly developed . . . ." The specimens from our locality are poorly preserved. The shell appears to be somewhat heavier and darker in color than specimens from elsewhere in the Sierra de Tlahualilo, the Sierra de Santa Ana and Sierra de la Peña described by Jones (1938, p. 107).

Specimens 42343 and 42344 are the more typical development of *Gryphaea washitaensis*. Specimen 42300 is close to the variety *kellumi* Jones. Specimens 42298, 42299, and 42312 are extremes of variation within the species and approach the end form of *G. corrugata* Say, which, as pointed out by Hill and Vaughan (1898, p. 62), is gradational with *G. washitaensis*.

Genus PECTEN Muller

Pecten spp.

(Pl. I, Figs. 13, 15, 17)

Diagnosis.—Four coarsely ribbed fragments of *Pecten* in Collection 53-K-20 are too poorly preserved for specific identification. The beak and hinge areas are missing in all of them. The ribs are slightly wider than the interspaces; both narrow toward the beak.

A plasteline impression of one specimen, an interior of nearly half the valve, shows the tops of the ribs broadly rounded with vertical sides and the bottoms of the interspaces flat. Another specimen has somewhat narrower interspaces which are rounded at the bottom.

Catalogue number.—UMMP 33148, 36813, 36814, and 36815.

Genus TRIGONARCA Conrad

Trigonarca sp. cf. *T. depressa* (White)

(Pl. III, Fig. 5)

1876. *Idonearca depressa* White, U.S. Geog. and Geol. Surv. West 100th Meridian, 4: 183, pl. 18, figs. 13a and b.
1893. *Trigonarca depressa* (White), Stanton, U.S. Geol. Surv. Bull., 106: 93, pl. 19, fig. 2
1908. *T. depressa* (White), Shimer and Blodgett, Amer. Journ. Sci., 4th Ser., 25: 62.

Diagnosis.—One rather well-preserved right valve was discovered in the matrix in the course of examining other specimens of the fauna under a binocu-

lar microscope. Its hinge area and interior are concealed, but the recrystallized shell material preserves in detail the shape and exterior sculpture of the valve.

Shell small, gibbous, irregularly trapezoidal to subovate in marginal outline; posterior half of the basal margin broadly arcuate, rounding anteriorly upward, and sharply rounding posteriorly to meet the posterior margin at the posterior radial angulation of the disk. Anterior margin regularly rounded up to the hinge line; posterior margin nearly straight, extending obliquely downward and backward, nearly equal in length to half the height of the shell. The posterior radial angulation is very pronounced on the lower third of the disk but disappears before reaching the middle and is not present in the umbonal region. The umbone, situated just anterior to the center of length of the shell, is gibbous and meets the hinge line at a right angle, extending horizontally from there nearly to the maximum depth of the valve, arching gently to that point which is above the middle of the disk.

Surface marked by 20 flat radiating ribs of nearly equal width, and narrow, sharply impressed interspaces between them; ribs largest near the posterior angulation, becoming obsolete anteriorly and posteriorly on the steep slopes near the margins.

Dimensions (of single valve).—Length 4.0 mm., height 3.0 mm., depth 1.2 mm.

Catalogue number.—UMMP 42313.

GASTROPODA

Genus TYLOSTOMA Sharpe 1849

Tylostoma sp.

(Pl. III, Figs. 6, 7, 9, 10)

Description.—Two internal molds are referred to this species. Each consists of the body whorl and the preceding one.

Shell elongate, medium to large, whorls convex, the body whorl constitutes most of the bulk; sutures deeply impressed on internal molds; varices indicated by faint to pronounced grooves in which the transverse edge of shell material is seen in the mold; aperture elongate lunate.

Dimensions.—UMMP 32622, height of two anterior whorls 55 mm., breadth of body whorl 33 mm., height of aperture 21 mm.; UMMP 42328, height of two anterior whorls 48 mm., breadth of body whorl 32 mm., height of aperture 25 mm., breadth of aperture 11 mm.

Hypotypes.—UMMP 32622 and 42328.

BIBLIOGRAPHY

Adkins, W. S. 1918. The Weno and Pawpaw Formations of the Texas Comanchean. Texas Univ. Bull., 1856: 1–172.

——. 1928. Handbook of Texas Cretaceous Fossils. Texas Univ. Bull., 2838: 1–385, pls. 1–37.

Bergquist, H. R., and W. A. Cobban. 1957. Mollusks of the Cretaceous, *In* Treatise on Marine Ecology and Paleoecology, No. 2, H. S. Ladd, ed., pp. 871–884.

Böse, E. 1918. On a New Ammonite Fauna of the Lower Turonian of Mexico. Texas Univ. Bull., 1856.

—— and O. A. Cavins. 1927. The Cretaceous and Tertiary of Southern Texas and Northern Mexico. Texas Univ. Bull., 2748: 1–142.

Boyle, C. B. 1893. Catalogue and Bibliography of North American Mesozoic Invertebrata. U.S. Geol. Surv. Bull., 102: 1–315.

Cobban, W. A., and J. B. Reeside, Jr. 1952. Correlation of the Cretaceous Formations of the Western Interior of the United States. Geol. Soc. Amer. Bull., 63: 1011–1044, chart 106, 2 text figs.

Cragin, F. W. 1893. A Contribution to the Invertebrate Paleontology of the Texas Cretaceous. Texas Geol. Surv. 4th Ann. Rept. iv + pp. 139-294, pls. 24–46.

Hill, R. T., and T. W. Vaughan. 1898. The Lower Cretaceous Gryphaeas of the Texas Region. U.S. Geol. Surv. Bull., 151: 1–139, pls. 1–35.

Imlay, R. W. 1944. Correlation of the Cretaceous Formations of the Greater Antilles, Central America, and Mexico. Geol. Soc. Amer. Bull., 55: 1005–1045, chart 10a, 2 pls., 1 text fig.

——. 1957. Paleoecology of Jurassic Seas in the Western Interior of the United States, *In* Treatise on Marine Ecology and Paleoecology, v. 2, H. S. Ladd, ed., pp. 469–504, 1 tab., 8 text figs.

Jones, T. S. 1938. Geology of Sierra de la Peña and Paleontology of the Indidura Formation, Coahuila, Mexico. Geol. Soc. Amer. Bull., 49: 69–150, pls. 2–13, 4 text figs.

Jourdy, E. 1924. Histoire Naturelle des Exogyres. Annales de Paléontologie, 13: 1–104, 13 pls.

Kellum, L. B. 1954. Geology of the Villareal Uplift, Sierra de Tlahualilo, Coahuila, Mexico. Geol. Soc. Amer. Bull., 65 (12) pt. 2: 1273.

——. 1956. Cretaceous Invertebrates of the Aurora Limestone. PMASAL, 41 (1955): 205–231, 7 pls., 1 text fig., 1 tab.

——, R. W. Imlay, and W. G. Kane. 1936. Evolution of the Coahuila Peninsula, Mexico. Part I. Relation of Structure, Stratigraphy and Igneous Activity to an Early Continental Margin. Geol. Soc. Amer. Bull., 47(7): 969–1008, 3 pls.

Matthews, W. H. 1951. Some Aspects of Reef Paleontology and Lithology in the Edwards Formation of Texas. Texas Jour. Sci., 2: 217–226.

Reinhart, P. W. 1943. Mesozoic and Cenozoic Arcidae from the Pacific Slope of North America. Geol. Soc. Amer. Spec. Paper, 47: 1–117, pls. 1–15, 3 text figs.

Robinson, W. I., and L. B. Kellum. 1941. Geology of Sierra de Tlahualilo, Durango. Geol. Soc. Amer. Bull., 52(12), pt. 2, pp. 1930–1931.

Shattuck, G. B. 1903. The Mollusca of the Buda Limestone with an Appendix on the Corals of the Buda Limestone. U.S. Geol. Surv. Bull., 205: 1–94, pls. 1–27, 1 text fig.

Stanton, T. W. 1893. The Colorado Formation and Its Invertebrate Fauna. U.S. Geol. Surv. Bull., 106: 1–288, pls. 1–45.

——. 1947. Studies of Some Comanche Pelecypods and Gastropods. U.S. Geol. Surv. Prof. Pap., 211: 1–116, pls. 1–67.

Stephenson, L. W. 1933. The Zone of *Exogyra cancellata* Traced Twenty-five Hundred Miles. Am. Assoc. Petroleum Geologists Bull., 17(11): 1351–1361.

——. 1952. Mollusks from the Pepper Shale Member of the Woodbine Formation McLennan County, Texas. U.S. Geol. Surv. Prof. Pap., 243-E: 57–68, 1 pl.

——. 1952. Larger Invertebrate Fossils of the Woodbine Formation (Cenomanian) of Texas. U.S. Geol. Survey Prof. Pap., 242: 1–226, pls. 4–59, 5 text figs.

White, C. A. 1884. Fossil Ostreidae of North America; and a Comparison of the Fossil with the Living Forms, *In* Powell, J. W., 4th Ann. Rept. of the U.S. Geol. Surv. to the Sec. of the Interior, 1882–83: 273–430, pls. 34–82.

Whitney, F. L. 1928. Bibliography and Index of North American Mesozoic Invertebrata. Am. Paleont., 12(48): 1–448.

EXPLANATION OF PLATE I

Page

Exogyra acroumbonata Kauffman n. sp., in press 42

Figs. 1 and 8. Exterior and posterior views of left valve (× 2). Holotype UMMP 42215 from the Graneros formation, Huerfano County, Colorado.

Figs. 2 and 9. Exterior and posterior views of left valve (× 3). Hypotype UMMP 42295 from the Indidura formation, Sierra de Tlahualilo, Coahuila.

Exogyra columbella Meek 42

Fig. 3. Exterior of left valve (× 1). Hypotype UMMP 42292 showing costae radiating from umbonal ridge depth of valve and the recurved beak.

Fig. 4. Exterior of left valve (× 1). Hypotype UMMP 42291, showing symmetrical, smooth variety.

Fig. 5. Interior of right valve (× 1). Hypotype UMMP 42301, showing slight extension on posterior side.

Fig. 6. Exterior of left valve (× 1). Hypotype UMMP 42293, showing radial costae.

Fig. 7. Interior of right valve (× 1). Hypotype UMMP 42302 showing concentric undulations and posterior extension.

Fig. 10. Posterior view of left valve, same specimen as Fig. 3 (× 1), showing recurved beak and depth of valve.

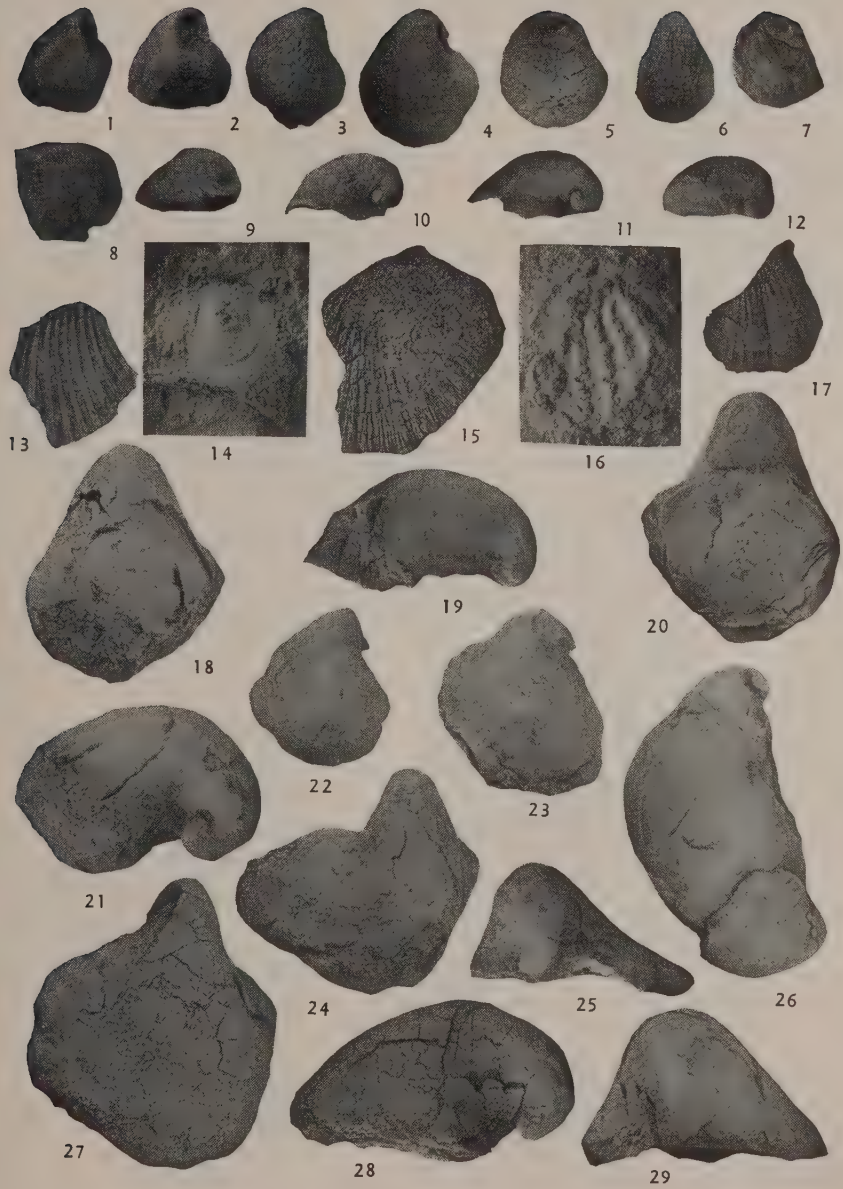
Fig. 11. Posterior view of left valve, same specimen as Fig. 4 (× 1), showing recurved beak and depth of valve.

Fig. 12. Posterior view of left valve, same specimen as Fig. 6 (× 1), showing recurved beak and depth of valve.

Pecten sp 46

FIG. 13. Interior of valve (× 1) Hypotype UMMP 33148, showing ribs wider than interspaces and both decreasing in width toward the umbone.
Inoceramus sp. 41
FIG. 14. Cast of natural mold of exterior, (× 4), Hypotype UMMP 42322, showing rounded outline and concentric undulations.
Pecten sp. 46
FIG. 15. Exterior of valve (× 1), Hypotype UMMP 36813, showing bifurcating ribs.
Plicatula subgurgitis Böse 41
FIG. 16. Interior of valve (× 3), Hypotype UMMP 42324, showing beaded radiating costae and concentric growth lines.
Pecten sp. 46
FIG. 17. Exterior of valve (× 1), Hypotype UMMP 36814, showing ribs and interspaces nearly equal over most of the disk.
Exogyra extenda n. sp. Kellum and Shubak 43
FIG. 18. Exterior of left valve (× 1), Holotype UMMP 42290, showing high beak, and symmetrical flare.
FIG. 19. Posterior of left valve (× 1), Hypotype UMMP 42289, showing recurved beak and depth of valve.
FIG. 20. Exterior of right valve (× 1), Holotype UMMP 42290, showing coil near umbo of right valve and radiating costae on umbo of left valve.
FIG. 21. Posterior of left valve (× 1), Holotype UMMP 42290, recurved beak and depth of valve.
Exogyra columbella Meek 42
FIG. 22. Exterior of left valve (× 2), Hypotype UMMP 42294, variety with curved umbonal ridge, narrower umbo, and smooth shell.
FIG. 23. Exterior of left valve (× 2), Hypotype UMMP 42326, showing costae on anterior slope of a broader variety.
Exogyra extenda n. sp. Kellum and Shubak 43
FIG. 24. Exterior of left valve (× 1), Hypotype UMMP 42309, showing specimen with wide flare of anterior slope.
FIG. 25. Dorsal view of left valve (× 1), same specimen as Fig. 24, showing deflection of the umbo.
Exogyra sp. 44
FIG. 26. Posterior view of left valve (× 1), Hypotype UMMP 42308, showing irregular, bulbous areas.
Exogyra extenda n. sp. Kellum and Shubak 43
FIG. 27. Exterior of left valve (× 1), Hypotype UMMP 42310, showing elevation of beak and flare of anterior and posterior slopes.
FIG. 28. Posterior view of left valve (× 1), same specimen as in Fig. 27, recurved beak and depth of valve.
FIG. 29. Dorsal view of left valve (× 1), same specimen as in Figs. 27 and 28, showing asymmetrical development of the umbo and disk.

PLATE I



EXPLANATION OF PLATE II

Page

Exogyra robusta n. sp. Kellum and Shubak..... 44

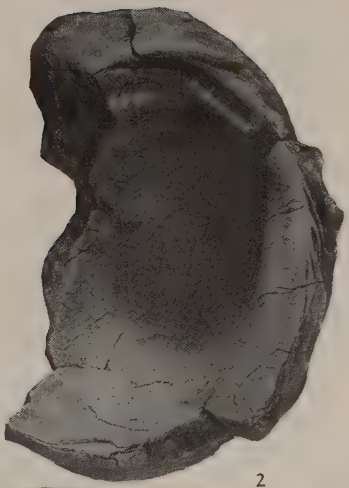
FIGS. 1 AND 4. Exterior and interior views of left valve (× 1), Holotype UMMP 42296, showing massive character of the shell.

Exogyra tlahualiloensis n. sp. Kellum and Shubak..... 42

FIGS. 2 AND 3. Interior and exterior views of left valve (× 1). Hypotype UMMP 42304, showing hinge and umbonal ridge.

PLATE II

1



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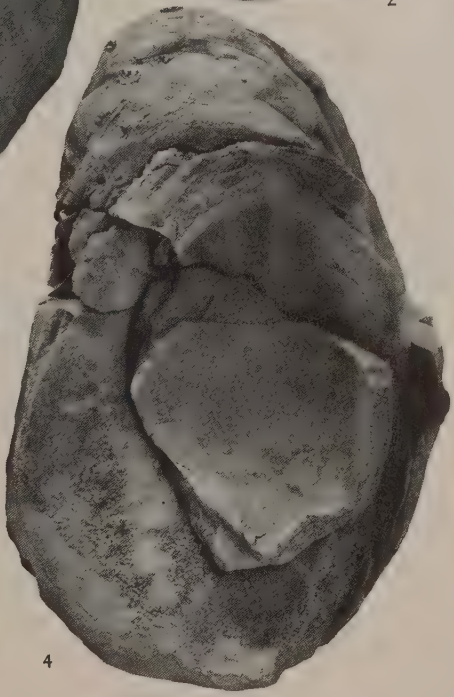


4

EXPLANATION OF PLATE III

Kingena wacoensis (Roemer) 40

FIG. 1. Brachial valve (× 1), Hypotype UMMP 33168.

Inoceramus sp. 44

FIG. 2. Mold of exterior of valve (× 1), Hypotype UMMP 32327.

Exogyra sp. 44

FIG. 3. Exterior of right valve (× 1), Hypotype UMMP 42329, showing concentric imbrications.

Inoceramus sp. 41

FIG. 4. Mold of interior of valve (× 2), Hypotype UMMP 42323, showing pointed beak and irregular concentric undulations.

Trigonarca sp. cf. *T. depressa* (White) 46

FIG. 5. Exterior of right valve (× 4), Hypotype UMMP 42313, showing trapezoidal form and radiating ribs.

Tylostoma sp. 47

FIGS. 6 AND 7. Posterior and anterior side views of internal mold (× 1), Hypotype UMMP 32622, showing varices and convexity of whorls.

FIGS. 9 AND 10. Posterior and apertural view of internal mold (× 1), Hypotype UMMP 42328, showing varix and convexity of whorls.

Exogyra tlahualiloensis n. sp. Kellum and Shubak 42

FIG. 8. Exterior of left valve (× 1), Hypotype UMMP 42305, showing umbonal ridge.

Exogyra robusta n. sp. Kellum and Shubak 44

FIG. 11. Posterior view of left valve (× 1), Hypotype UMMP 42296, showing massive character, depth of valve, and recurving beak.

PLATE III

EXPLANATION OF PLATE IV

Exogyra tlahualiloensis Kellum and Shubak 42

FIG. 1. Exterior of left valve (× 1), Hyptoype UMMP 42303, showing umbonal ridge.

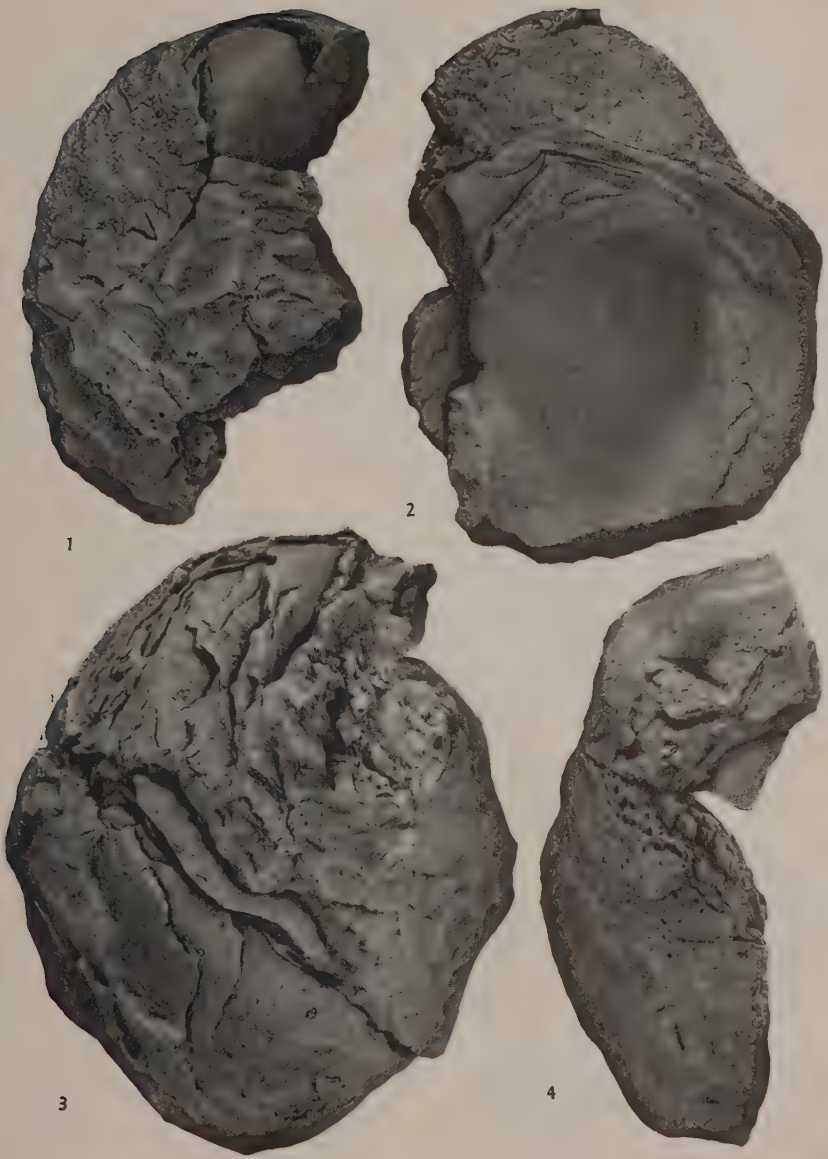
FIG. 2. Interior of left valve (× 1), Hypotype UMMP 42305, a heavier variety of the species.

FIG. 3. Exterior of left valve (× 1), Holotype UMMP 42297, showing umbonal ridge and ovate outline of the shell.

Exogyra sp. 44

FIG. 4. Exterior of fragment of left valve (× 1), Hypotype UMMP 42306, showing shape of anterior margin.

PLATE IV



EXPLANATION OF PLATE V

Gryphaea washitaensis Hill 45

FIGS. 1 AND 2. Exteriors of right and left valves (× 1). Hypotype UMMP 42299, showing a variant of the species.

FIGS. 3 AND 9. Exterior of left and right valves (× 1). Hypotype UMMP 42312, showing a variant of the species.

FIGS. 4 AND 5. Exterior of right and left valves (× 1). Hypotype UMMP 42298, showing variant of the species.

Exogyra tlahualiloensis n. sp. Kellum and Shubak. 42

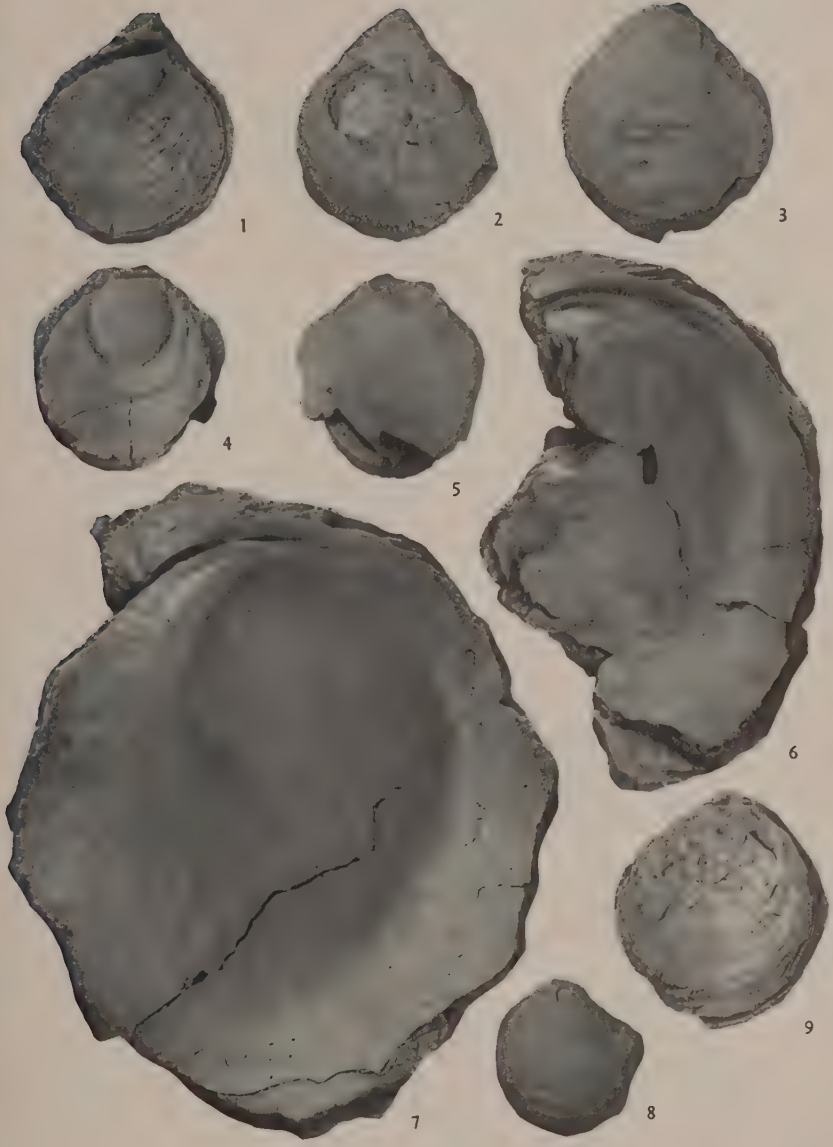
FIG. 6. Interior of left valve illustrated on Plate IV, Fig. 1, Hypotype UMMP 42303, showing hinge area and free anterior margin.

FIG. 7. Interior of left valve illustrated on Plate IV, No. 3, Holotype UMMP 42297, showing hinge area and recurved beak.

Gryphaea washitaensis Hill. 45

FIG. 8. Exterior of left valve (× 2), Hypotype UMMP 42300, variant approaching *G. washitaensis* var. Kellumi Jones.

PLATE V



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PALEONTOLOGY

UPPER PLIOCENE GEOLOGY AND VERTEBRATE PALEONTOLOGY OF PART OF THE MEADE BASIN, KANSAS

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The Meade Basin of southwestern Kansas, or Meade trough as it was called by Erasmus Haworth in 1896, has long been an area of geologic interest. Fossil material, collected from Upper Pliocene deposits, was described by Claude W. Hibbard in 1938, and in the ensuing years late Cenozoic deposits of Upper Pliocene and Pleistocene age have been intensively studied. The Upper Pliocene fauna indicates an expected difference between the climate extant at that time and that of the Pleistocene or Recent.

The earliest detailed geologic study of this and surrounding areas was presented by H. T. U. Smith in 1940, and from it much of the supporting material for this report has been obtained. The term "basin" was applied to the area by John C. Frye (1940, p. 6) and has been used in all subsequent work. The Meade Basin extends north-northeast for about 30 miles across central Meade County and northward into southwestern Ford County (Smith, 1940, p. 133). The area of the present study is situated southwest of Meade County State Park, 8 miles south and 6 miles west of Meade, Kansas, as shown in Fig. 1, which is the first detailed map of the type area of the Rexroad formation.

Although this paper is concerned mainly with Upper Pliocene geology and paleontology, it was necessary to map the Pleistocene sequence in order to determine the limits of the Upper Pliocene deposits. In the summer of 1959 I was a member of a field party of The University of Michigan Museum of Paleontology under the direction of Claude W. Hibbard. During this period the geology was plotted on a base map which had been prepared from aerial photographs. Of the various problems encountered during the period of mapping, one of major importance was that, in any one location, the geology was

usually exposed on only the outside of a stream meander. This side was typically a vertical wall up to 30 feet high whereas the opposite side would be a gentle slope, covered with soil, grass, and sagebrush, leading up to the interstream areas. It was rarely possible to measure strike and dip directly. In Sec. 22, T. 33 S., R. 29 W., the beds are highly variable in a lateral direction, and it was often difficult to find a well-marked horizon that extended over a usable distance. While resistant beds, i.e., consolidated sand and gravel, and caliche are present, they do not crop out continuously over large areas, but are usually found as rubble on slopes. The finer sediments of the deposits of the different formations are not lithologically distinct. These factors, combined with the slight dip of the beds in general, hindered mapping. The main basis for correlation of beds was stratigraphic position.

Stratigraphy

Pre-Cenozoic rocks.—The bed rock of the area is the Permian Whitehorse formation (Smith, 1940, p. 32). These red beds crop out in the east side of the bed of Crooked Creek about 4 miles east of the area mapped. The Permian rocks contain layers of salt and anhydrite, the solution of which has caused some solution depressions in the surrounding area (Frye and Schoff, 1942, p. 38). The most pronounced of these features are found in Clark County, to the east. There, in St. Jacob's Well, a slump block of the Ogallala has a dip of 35° (Smith, 1940, p. 131).

Cenozoic rocks.—Rocks representing the time span from the Lower Pliocene to Recent epochs are found in the Meade Basin. These consist mainly of clastic sediments whose particle sizes range from gravel to clay. Sand and gravel conglomerates may be held together with a calcium carbonate cement, but most of the sediments are unconsolidated. Caliche is the chief nonclastic deposit and is most commonly seen as nodules and stringers dispersed in poorly defined zones throughout the deposits. It may be, however, concentrated into definite bands 2 to 3 feet thick. The other nonclastic deposit of note is that of lignite, which occurs in the Rexroad formation at locality 3 (Fig. 1).

Lower Pliocene.—Deposits of the Lower Pliocene Laverne formation are not exposed in the area mapped. The nearest exposures of the Laverne formation are along the Cimarron River in southwestern

Meade County and in southeastern Seward County (Byrne and McLaughlin, 1948, pl. I).

Middle Pliocene.—The Middle Pliocene Ogallala formation crops out on the east side of Crooked Creek 4 miles east of the area mapped, and probably continues under it. Ogallala deposits have a great areal extent, being more or less continuous from the Panhandle of Texas to the Platte Valley of Nebraska. The formation is a stream-laid gravel and silt with lesser amounts of clay, which was derived from the Rocky Mountain Region (Smith, 1940, p. 39). In Meade County, the top of the formation is a light gray cap rock formed by secondary calcium carbonate cement. Here, the Ogallala formation is 103 feet thick (Smith, 1940, p. 67).

Upper Pliocene.—The Rexroad formation is found west of Crooked Creek in valleys where the streams have cut down through the overlying deposits, and generally occurs as discontinuous exposures. This formation was described by H. T. U. Smith (1940, p. 95) from exposures along tributaries of Crooked Creek in Meade County, Kansas, as "consisting of alternating beds of gray to reddish mudstone, buff sandy silt, rusty sand and gravel, and a few thin seams of lignite. The gravel is locally cemented to form a conglomerate very similar to that found in the Ogallala, but contains some calcareous pebbles seemingly reworked from the Ogallala." Part of this description pertained to beds of Pleistocene age, especially that referring to the consolidated sand and gravel. The sand and gravel exposed in this area is not of the Rexroad formation, but rather of the basal Pleistocene deposits (Frye and Hibbard, 1941, p. 407).

The most complete section of Rexroad deposits is exposed near the mouth of Wolf Canyon, along the Cimarron River in the southwestern corner of Meade County. In this area, Sec. 7, T. 35 S., R. 30 W., Meade County, Kansas, the Rexroad formation is 86 feet thick and rests directly on the Laverne formation (Byrne and McLaughlin, 1948, p. 74). The following description of the Rexroad formation is based on Byrne and McLaughlin (1948, p. 73). In Wolf Canyon the Rexroad consists of a lower sand and gravel part, a middle (transitional) coarse gravel to silt sequence, and an upper unit of silt and clay with nodules of caliche. The thickness of the basal part is variable because these deposits are channeled into the underlying material. The gravels consist of particles derived from igneous rocks, mainly feldspar and quartz with some mica. The sand is mainly quartz.

When the sand and gravel is locally cemented with calcium carbonate a conspicuous ledge-forming rock results. This ledge rock is coarser grained, contains less calcium carbonate, and weathers to a smoother surface than that of the Ogallala. The middle sequence is transitional to the lower gravel and the upper silt and clay. It is a poorly bedded, moderately indurated, heterogeneous accumulation of reddish clay, silt, sand, and gravel, with locally abundant nodules and stringers of caliche. The upper part consists of finer deposits, silts, fine sands, and clays which range in color from brown to various shades of gray. Near the top is often a bed of hard, cherty caliche, 2 feet thick, which weathers to irregular, rough, pitted boulders.

The Saw Rock Canyon fauna, known from a locality near the center of the west section line of Sec. 36, T. 34 S., R. 31 W., Seward County, Kansas, comes from the XI member near the bottom of the Rexroad formation (Hibbard, 1949, p. 93).

At the Fox Canyon fossil locality (UM-K1-47) in Sec. 35, T. 34 S., R. 30 W., Meade County, Kansas, the Rexroad deposits dip south toward the Cimarron River. The fossils occur in a local pocket of rusty gray to reddish tan sandy silt, which is 17 feet below a massive caliche zone 3 to 5 feet thick (Hibbard, 1950, p. 120).

The Rexroad deposits at the Keefe Canyon quarry (locality 22) in Sec. 3, T. 35 S., R. 30 W., consist of a reddish buff to buff silt. The silt contains stringers and nodules of caliche, and, in places, a massive caliche zone 2 feet thick occurs near the upper third of the exposure. The fossils were recovered from an artesian sand tube and its surrounding basin about 6 feet below the caliche horizon. The base of the deposits is not visible. The exposure is about 45 feet thick here, but a drilled section in the Rexroad in the SE^1_4, NE^1_4 Sec. 33, T. 34 S., R. 30 W., shows a thickness of 182 feet (Hibbard and Riggs, 1949, pp. 831–833).

The deposits in the Wendell Fox pasture contain one of the most recently developed Rexroad fossil quarries in the area. The following section was measured at that locality (K3, Fig. 1).

MEASURED SECTION NO. 1

In the SW¼, SW¼ Sec. 33, T. 33 S., R. 29 W., Meade Co., Kansas (locality UM-K3-53)

	Thickness in Feet
6. Topsoil	0.66
Rexroad Formation	
5. Caliche, massive	1.13

4. Silt, sandy, light green	7.13
3. Silt, sandy, light brown. Main fossil horizon	1.00
2. Clay, silty, green-gray, becomes lighter toward bottom	3.50
1. Caliche, with sand particles and clay, white. Base not exposed	0.85
Bed of Shorts Creek, total thickness	14.27

MEASURED SECTION NO. 2

Upstream from locality UM-K3-53, in the SE¼, SE¼ Sec. 32, T. 33 S., R. 29 W., Meade Co., Kansas

	Thickness in Feet
8. Topsoil	5.00
Rexroad Formation	
7. Silt, sandy, light tan, moderately indurated with calcium carbonate	2.00
6. Silt, sandy, brown, with caliche concentrated in lower one third	16.00
5. Silt, sandy, light brown, friable, with green clay layer 2 inches thick in middle. Irregular massive caliche rests locally on clay layer	22.00
4. Silt, sandy, brown, coarser near top, with irregular nodular caliche 10 inches below top	2.50
3. Silt, sandy, and silt, light green-gray, with irregular 4-inch lime-enriched zone about 10 inches below top	2.55
2. Silt, brownish green, with calcareous material. Correlates with unit 3 of measured section No. 1	0.66
1. Silt, greenish gray, base not exposed	0.25
Bed of Shorts Creek, total thickness	50.96

The deposits of measured section No. 2 are essentially continuous along Shorts Creek in Secs. 32 and 33, T. 33 S., R. 29 W. (Fig. 1). In this area there is not the great degree of lateral variation that is found in the Rexroad sediments of Sec. 22, T. 33 S., R. 29 W. To the present, fossils have been found concentrated in this area at only locality UM-K3-53. The beds surrounding this locality dip generally east to southeast, toward the main fault along Crooked Creek. From measured section Nos. 1 and 2 it may be seen that there are two zones of massive caliche development above the fossil horizon.

In the type area of the Rexroad formation, Sec. 22, T. 33 S., R. 29 W., Meade County, Kansas, the sediments show great lateral variation. The beds dip southeast, so that by progressing downstream, one moves upward in the section (Fig. 1). Just upstream from the type

locality of the Rexroad local fauna (locality 3, Fig. 1), the sediments of the Rexroad formation consist of an orange-buff quartz sand which is indurated by calcium carbonate cement and contains scattered pebbles up to 2 inches in diameter. Stratigraphically below this deposit is a coarse sand and fine gravel, with some manganese stain, which exhibits cross-bedding. The base of this deposit is not exposed.

MEASURED SECTION NO. 3

In the W½, SW¼ Sec. 22, T. 33 S., R. 29 W., Meade Co., Kansas (locality 3, Fig. 1)

	Thickness in Feet
3. Covered slope interval	10.00
Rexroad Formation	
2. Clay, sandy, light gray, indurated, with a limonitic layer about three feet from the bottom. Weathers greenish, fresh surface is brownish gray	7.50
1. Lignitic zone. Brown lignitic matter interbedded with gray-brown clay. Lower one half is mostly brown clay with some sandy silt. The lignitic layer is local, grades laterally into gray clays and fine, limonite-stained sand. Base not exposed. Main fossil horizon	5.50
Bed of Stream, total thickness	23.00

Downstream from locality 3, in Sec. 22, T. 33 S., R. 29 W., 1400′ E., 930′ N. of SW. corner, there is a massive caliche about 3 feet thick. This caliche is stratigraphically above the fossil deposits at locality 3 and below the beds containing the Bender local fauna. An account of the Bender local fauna is given by Taylor (1960).

At the Bender faunal locality the basal sand and gravel member (Angell) of the Ballard formation does not overlie all of the Rexroad deposits. Instead, the Missler silt member of the Ballard directly overlies the Rexroad formation. (Pl. 1, Fig. 1). North and south of this point, the Angell member is found lying between the Missler silts and the Rexroad deposits. The following measured section was taken at the point where the Missler silts directly overlie a Rexroad "high." This situation is not unique. Similar conditions were found elsewhere in the area mapped, notably in Sec. 32, T. 33 S., R. 29 W., 900′ W., 2800′ S. of the NE. corner (Pl. I, Fig. 2).

MEASURED SECTION NO. 4

In SW corner of SW¼, SE¼ Sec. 22, T. 33 S., R. 29 W., Meade Co., Kansas (Bender local fauna locality)

	Thickness in Feet
Ballard Formation	
Missler member	
13. Silt and fine sand, brown to buff, friable	1.00
12. Silt, containing caliche, nodular	0.16
11. Silt, sandy, brown with limonite stain	0.91
10. Silt and fine sand, brown to buff, indurated with calcareous cement	0.33
9. Silt, sandy, limonitic, indurated	1.66
8. Silty, sandy, brown with green clay	0.60
7. Clay, green-gray, friable, with caliche stringers	0.66
6. Silt, sandy, green-gray, friable, limonite stain	1.00
5. Silt, with much calcium carbonate, fine, green-gray, friable. Found at contact between Angell member and Rexroad formation immediately to the north and south.	1.25
Disconformity	
Rexroad Formation	
4. Bender fauna zone, silt, brown to dark gray with gastropods.	1.33
3. Silt, green-gray, with limonite stain.	1.00
2. Silt, containing caliche, nodular.	0.25
1. Silt, green-gray, limonite stain, with caliche nodules becoming more concentrated at bottom. Base not exposed.	0.91
Bed of Stream, total thickness	11.16

It is interesting to note the presence of a well-defined calcium carbonate layer at the contact between the Ballard and Rexroad formations, a feature which is not everywhere found in this stratigraphic position.

There is one massive caliche exposed in the type area of the Rexroad formation. It is stratigraphically above the fossil deposits of locality 3. This caliche is thicker than those mentioned in measured section No. 2 in the Wendell Fox pasture. Measured section No. 2 shows two massive caliches, units 5 and 6, which are separated by about 10 feet of sandy silt. In this area, then, there were two periods of caliche formation with an intervening period of deposition. Upstream from the location of measured section No. 2, in SW¼ Sec. 32, there is a massive caliche 3 to 4 feet thick. It may be that the two

caliche layers of measured section No. 2 coalesce further upstream into a unit similar in thickness to that found in the type area of the Rexroad formation. If this is true, the caliche in the Wendell Fox pasture and the one at the Rexroad type area may represent the same period of massive caliche development. In any case, the fossils found at both localities were deposited prior to the development of the massive caliches.

Pleistocene.—Pleistocene deposits in the Meade Basin consist of two main types. The earlier are widespread sheet deposits of the Meade Group. This group is composed of the Ballard and Crooked Creek formations, the Ballard being the older of the two. Much of the upland surface in the area surrounding Meade, Kansas consists of the Crooked Creek formation.

The second type of deposits, the Sanborn Group (Hibbard, 1958), consists of valley and sinkhole fillings which include the Kingsdown and Vanhem formations. Coarse material, indicating stream deposition, may be present in these beds, but the sediments exhibit no regular succession of coarse to fine particle size. These deposits are, generally, not so widespread as those of the earlier Pleistocene.

Structural relations.—From Fig. 1 it may be seen that the dip of the beds generally increases from west to east. It is also evident that the dip of the Rexroad deposits is generally greater than those of the overlying formations. The sediments of the Crooked Creek formation are mainly flat-lying.

Two small faults may be found on Fig. 1. One of these faults is developed in the Rexroad formation at locality UM-K3-53 (K3, Fig. 1). It strikes N. 72° E., dips 64° SE., and is downthrown to the southeast. The net slip is about 1 foot. The other fault disrupts Ballard and Rexroad deposits in the NW^1_4, SE^1_4 Sec. 22, T. 33 S., R. 29 W.; it strikes N. 46° E., dips 56° SE., and is downthrown to the southeast. The net slip is about 3 feet.

I interpret the faults as adjustment features associated with the main Crooked Creek fault to the east. The first of the small faults implies post-Pliocene movement, while the second is the result of post-Ballard activity. It is possible that both faults represent the later movement.

Haworth believed the Meade Basin to have been formed by a fault, the west side being the downthrown (Smith, 1940, p. 133). The present Crooked Creek is thought to flow generally along this fault (Smith, 1940, p. 135). Evidence for a fault can be seen in Crooked

Creek valley, 4 miles east of the area mapped. On the east side of Crooked Creek the Permian red beds are exposed at the bed of the stream. The red beds are overlain by the Ogallala formation, which is covered by the upper part of the Crooked Creek formation.

On June 13, 1942, a water well was drilled on the west side of Crooked Creek valley on the George Roberts farm in the NW¼, NW¼ Sec. 20, T. 33 S., R. 28 W. Water-bearing gravel was reached at a depth of 260-280 feet, and at that point salt water began flowing in the well at a rate of about 1,000 gallons per minute (Hibbard, field notes, June 13, 1942, p. 113), suggesting that the Permian bed rock may not have been much deeper. This would give at least 280 feet of displacement along the Crooked Creek fault. As a result of this movement a well-defined scarp, 75–100 feet high, has formed on the east side of the fault.

The presence of the fault is the main reason that the Rexroad deposits are found west of Crooked Creek in the Meade Basin (Frye and Hibbard, 1941, p. 395). Pleistocene movement along the fault is indicated by the presence of the upper part of the Crooked Creek formation on the eastern or upthrown side, whereas west of the scarp those deposits are buried beneath valley fill 50–75 feet below the upper contact. For further discussion of the Crooked Creek fault see Smith (1940) and Frye and Hibbard (1941).

Systematic Description

The fossils to be discussed in this section have been chosen for their paleontologic significance. Many of the specimens, including those from locality UM-K3-53, have not been described previously. The specimens are now in the following institutions: Chicago Natural History Museum (CNHM); University of Kansas Museum of Natural History (KUMNH); and The University of Michigan Museum of Paleontology (UMMP).

ORDER RODENTIA

Family Castoridae

Dipoides rexroadensis Hibbard and Riggs

(Fig. 2*A–P*)

Dipoides rexroadensis Hibbard and Riggs, 1949, Geol. Soc. Amer., Bull., 60: 835, fig. 1*G*.
D. rexroadensis Hibbard, Shotwell, 1955, Jour. Paleont., 29: 135.

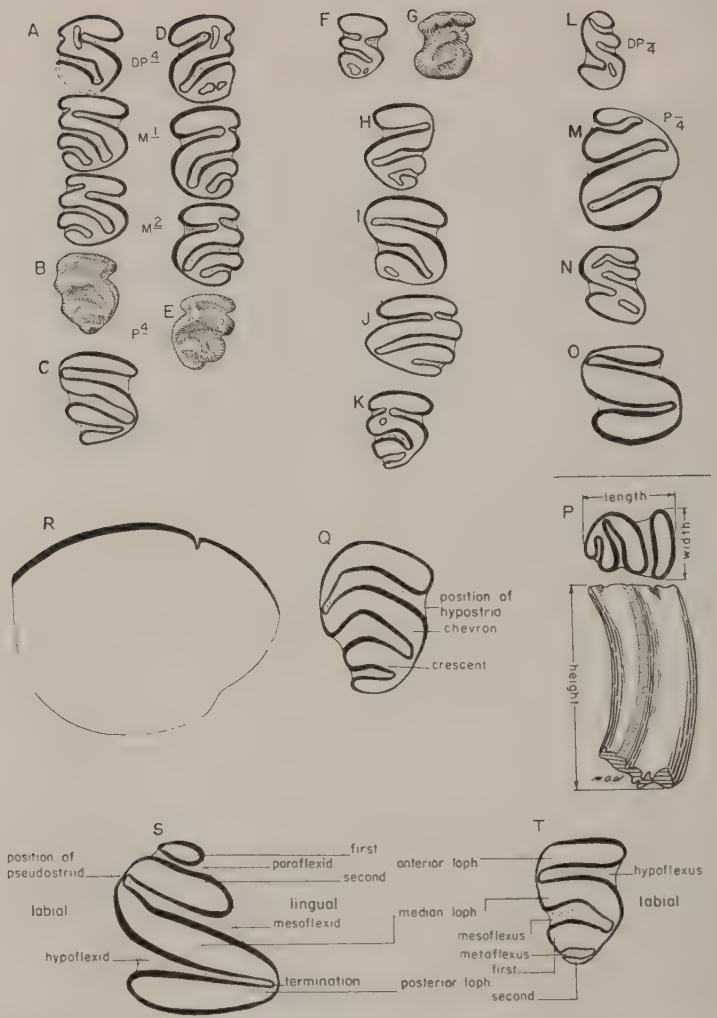

FIG. 2. *A–O*, *Dipoides rexroadensis* Hibbard and Riggs; *A–E*, UMMP 41149; *A*, right maxillary fragment, DP^4–M^2; B, RP^4; *C*, pattern at base of *B*; *D*, associated LDP^4–M^2; *E*, LP^4; *F*, UMMP 41153, RDP^4; *G*, UMMP 41153, unworn RDP^4; *H*, UMMP 41290, LM^1; *I*, UMMP 41153, RM^1; *J*, KUMNH 7281, LP^4; *K*, UMMP 41290, RP^4; *L*, UMMP 41290, LDP_4; *M*, KUMNH 7281, RP_4; *N*, UMMP 41290, left lower molar; *O*, KUMNH 7281, left lower molar; *P*, UMMP 35094, LM^2. *Q–T*, *Procastoroides sweeti* Barbour and Schultz; *Q*, UMMP 41290, RM^3; *R*, UMMP 41150, left upper incisor, cross-section; *S*, UMMP 42314, LP_4; *T*, KUMNH 3939, RM^3. All ×-2.

Since 1938, when the first mention was made of a beaver from the deposits of the Meade Basin, much additional material has been collected. None of the specimens recovered with the Rexroad fauna has been extensively described or figured. It is now possible to indicate the range of variation found in the remains of *Dipoides rexroadensis* and *Procastoroides sweeti* Barbour and Schultz from the above area, and to submit some remarks concerning the phylogenetic position of these beavers.

Terminology.—In discussing the teeth of these beavers I have used the dental terminology applied to those animals by Stirton (1935, p. 392), which was expanded by Shotwell (1955, p. 130). The terms that follow are illustrated by Fig. 2*P*, *Q*, *S*, and *T*.

Many beaver teeth consist of three lophs, an anterior, a median, and a posterior loph (Fig. 2*S*, *T*). The anterior loph of P_4 is divided by the paraflexid into two parts, a first and a second anterior loph (Fig. 2*S*). The first anterior loph is the more anterior of the two. Similarly, the posterior loph of M_3^2 may be divided into a first and a second posterior loph by the metaflexus (Fig. 2*T*). Lophs may be *inflated* or *uninflated*. The inflated condition exists when the two bands of enamel that make up its sides are not parallel (posterior loph of Fig. 2*S*). When the enamel bands are parallel, the loph is uninflated, as in the second anterior loph of Fig. 2*S*. When a loph possesses curvature, either concave or convex anteriorly, it is referred to as *crescentic* (Fig. 2*Q*). If the curvature is so sharp and abrupt that it has a decided point or apex it is a *chevron* (Fig. 2*Q*).

Flexi and flexids are infoldings of enamel which separate the lophs. *Flexus* refers to that of an upper, *flexid* to that of a lower tooth. The space between the enamel infolds of the flexus or flexid is filled with cement. The internal end of a flexus or flexid is called the *termination* (Fig. 2*S*). It can be either flattened, rounded, or narrowed. The termination *abuts* when it touches the enamel of the side of the tooth opposite that on which the infold originates. A *fossette*, usually a roughly circular body of enamel which is surrounded by dentine, is shown in Fig. 2*A*. In a lower tooth, the counterpart of a fossette is a *fossettid*.

A *stria* or *striid* is a groove, filled with cement, which results from the formation of a flexus or flexid. A stria (Fig. 2*Q*) occurs on an upper tooth and a striid on a lower. *Pseudostria* and *pseudostriid*, terms presented here for the first time, are found on the enamel of the tooth wall in conjunction with a tightly abutting termination and are used to designate areas where the enamel of the wall of the tooth has become greatly thinned or worn through (Fig. 2*S*). This allows the enamel of the termination to be seen in a lateral view. Some of these are so well defined that at first they appear to be striae or striids, as though the cement associated with flexi and flexids had broken through the tooth wall. The presence of pseudostriae and pseudostriids may represent an evolutionary stage intermediate to one in which the tooth wall is penetrated by flexi or flexids, as is shown by the teeth of *Castoroides ohioensis* Foster. Other terms used are either commonly understood or self-explanatory.

Holotype.—The holotype, KUMNH 7693, a LM^1 ?, was recovered from Upper Pliocene deposits at locality 22, SW^1_4, SW^1_4 Sec. 34, T. 34 S., R. 30 W., in Keefe Canyon, Meade County, Kansas.

Referred material.—Collected at locality 22 were KUMNH 7281, RP_4,

LP^4, $RM^{1?}$, and a lower molar. At locality 8, $W^1/_2$, $SW^1/_4$ Sec. 22, T. 33 S., R. 29 W., Rexroad Ranch, Meade County, Kansas, were UMMP 41149, associated right and left upper dentition, DP^4, P^4-M^2; UMMP 41158 RDP^4, LDP^4, LP^4, $RM^{1?}$; and at locality UM-K8-53, $SW^1/_4$, $SW^1/_4$ Sec. 35, T. 33 S., R. 29 W., Wendell Fox Pasture, Meade County, Kansas, UMMP 38455 LM^2, UMMP 41290, LDP_4, two RP^4, one LP^4, two LM^1, and a lower molar.

Diagnosis of species.—Since the holotype of the species was named from only one specimen, a diagnosis based on the holotype and the referred material seems worth while. The teeth of *Dipoides rexroadensis* are larger than those of the other species of the genus. Tab. 1; cf. Shotwell, 1955, tab. 2. When present the paraflexus commonly passes anterior to the hypoflexus. The width of P^4 is generally not greater than the length, contrary to that in *D. metae* Shotwell and *D. stirtoni* Wilson (see Shotwell, 1955, tab. 2). In none of the 6 P^4's examined was the anterior loph completely isolated by the entrance of the hypoflexus, as is found in *D. wilsoni* Hibbard (Hibbard, 1952, fig. 5). In both upper and lower premolar, *D. wilsoni* seems more variable than does *D. rexroadensis*. In P^4-M^2 of *D. rexroadensis*, the mesoflexus is curved more posteriorly than in those teeth of *D. wilsoni*. This situation is especially evident in P^4. No other species of the genus is known to be found in the same stratigraphic position as *D. rexroadensis*.

Tooth variation.—The variation of the teeth of *Dipoides rexroadensis* examined does not seem to be so great as that found in the teeth of *D. wilsoni*. The dental variation found in other species of the genus is discussed by Shotwell (1955). Shotwell (1955, p. 129) mentions that *D. rexroadensis* may belong to a different genus. As a result of this study, I believe that the tooth variation of *D. rexroadensis* is well within the range of that shown by the genus, although the species is distinct.

Upper deciduous premolar.—In UMMP 41149, the only maxillary fragment available (Fig. 2*A*), DP^4 is in position, along with M^1 and M^2. The molars are in a fairly early stage of wear with parastria and metastria still present. There were 4 DP^4's available for study (Fig. 2*A*, *D*, *F*, and *G*). One of these (Fig. 2*G*) is unworn. The parastria, hypostria, and mesostria are present in all. A metastria is present in the unworn tooth. In each tooth, the parastria is shorter than the metastria and would disappear at an earlier stage of wear. In 2 of the 3 worn teeth, a hypofossette is present (Fig. 2*A*, *D*). Two metafossettes are present in each of the teeth in Fig. 2*D* and *F*. In all of the teeth, the anterior loph is generally directed anterolingually and inflated lingually. The median loph is more or less crescentic and convex anteriorly. The posterior loph is inflated labially.

The paraflexus is short in all DP^4's and extends lingually or posterolingually. The termination of the paraflexus is rounded. In 2 of the worn teeth, the termination of the paraflexus is separated from a hypofossette by a tract of dentine (Fig. 2*A*, *D*).

The hypoflexus trends anterolabially or labially. Its termination may be rounded or flat and separated to a greater or lesser degree from the enamel of the hypofossette.

The mesoflexus is directed slightly posterolingually, but near the midline

TABLE I

MEASUREMENTS* OF TEETH OF *Dipoides rexroadensis*

Tooth	Mean Length	Mean Width	Range of Length	Range of Width	Number of Specimens
DP^4	5.7	4.4	5.7 ±	4.3–4.5	2
P^4	5.1	4.1	4.5–5.5	3.0–6.0	6
M^1	5.8	4.7	5.3–6.3	4.3–6.0	4
M^2	5.2	4.5	5.2–5.4	4.2–4.8	3

* In millimeters. For orientation of teeth during measurement see Fig. 2P. Most of the measured teeth were in an early stage of wear.

of the tooth, it turns more posteriorly. The termination of the mesoflexus is flat or rounded and does not abut tightly against the enamel of the tooth wall. The position of the metafossettes is shown in Fig. 2*D* and *F*.

Upper premolar.—Seven P^4's were collected, of which 4 are shown in Fig. 2*B*, *E*, *J*, and *K*. Fig. 2*C* shows the pattern at the base of Fig. 2*B*. The parastria, hypostria, mesostria, and metastria are present on all teeth. The metastria may disappear at the base of the tooth. In only 2 specimens does the parastria persist to the base of the tooth, a feature which is most significant in KUMNH 7281 from the Keefe Canyon locality (Fig. 2*J*). This tooth has a height of 16 mm., whereas that of the others is, at most, 12 mm. One specimen (Fig. 2*K*) has a fossette in the labial part of the median loph. In all teeth the anterior loph is crescentic, convex anteriorly as is the median loph. The posterior loph is inflated labially.

The paraflexus is usually directed slightly anterolabially in P^4. Its termination is flat or rounded and does not touch the enamel of the hypoflexus.

The hypoflexus generally extends anterolabially to a termination which is rounded or flattened. At the base of the tooth, the hypoflexus usually reaches the labial side of the tooth, and the termination may abut tightly with the wall enamel.

The mesoflexus trends posterolingually and may have the shape of either a broad or a tight curve. Its termination may be either flat or rounded, and in most cases does not abut tightly against the lingual wall of the tooth. This situation is found at both the occlusal surface and the base of the tooth.

The metaflexus is variable. It trends more or less labially and is often not present at the base of the tooth. When the metaflexus is present at the base, the tooth is usually short, the base probably having been broken off. The termination of the metaflexus is rounded and usually does not abut tightly with the enamel of the labial tooth wall.

Upper first and second molars.—Eleven M^1–M^2's were available for study, 7 of which are illustrated in Fig. 2*A*, *D*, *H*, *I*, and *P*. The teeth are subequal in size, M^1 being the largest. Only the hypostria and mesostria persist to the base of all of these teeth. In little-worn specimens, the parastria and metastria are

also present, the parastria extending further down the side of the tooth than the metastria, but never to the base. In UMMP 41149, the parastria and metastria are longer in M^3 than in M^4. This suggests that at a given instant of time, M^3 may be in a more advanced stage of wear than M^4. UMMP 35004 (Fig. 2*P*) shows the hypoflexus extending completely across the tooth in an early stage of wear. This condition would disappear as wear progressed. The anterior loph is inflated lingually, or is crescentic, convex anteriorly. The posterior enamel band of the median loph of M^4 appears as a rather smooth curve (Fig. 2*A* and *D*) while that of M^3 has a sharp bend, and is more like a chevron. The posterior loph is inflated labially.

In M^3 and M^4 the paraflexus, present in early stages of wear, is directed anterolingually. It is shorter in M^4 than in M^3. The termination of the paraflexus is rounded and overlaps anteriorly that of the hypoflexus in M^4 (Fig. 2*A* and *D*). In M^3 the termination of the paraflexus is narrowed and does not overlap anteriorly that of the hypoflexus. This situation may be correlated with the idea that M^3 is worn down first, causing the paraflexus to disappear in M^3 before it does in M^4.

The hypoflexus commonly extends anterolabially to a termination which may be rounded or flat. At the occlusal surface, no M^4 or M^3 shows the termination of the hypoflexus abutting tightly to the enamel of the labial tooth wall. At the base of the tooth the abutment is often tight.

The mesoflexus has either the shape of a crescent, convex anteriorly, or that of a chevron. It terminates on the lingual side of the tooth. The curve seems to be smoother in M^4. The termination of the mesoflexus is commonly flattened but does not abut tightly, in all cases, with the lingual wall enamel at either the occlusal surface or the base of the tooth.

Lower deciduous premolars.—Only 1 DP_4, UMMP 41290, has been collected (Fig. 2*L*). The pattern is generally similar to that of an LDP_4 of *Dipodies weidei* illustrated by Shotwell (1955, Fig. 2A). The Rexroad tooth is larger than that of *D. smithi*.

The parastriid, mesostriid, and hypostriid are present, but do not persist to the base of the tooth. The parastriid is the shortest, the hypostriid the longest of the striids. The first anterior loph is inflated lingually. The second anterior loph is crescentic, concave anteriorly, as is the median loph. The posterior loph is inflated and contains a hypofossettid.

The paraflexid curves anterolabially to a narrow termination which abuts tightly against the labial wall enamel. The mesoflexid extends anterolabially across only half of the tooth and the termination is rounded. The hypoflexid is directed posterolingually across only the labial half of the tooth and bears a flat termination. The termination is separated by dentine from the anterolabially directed hypofossettid. The hypofossettid is surrounded by dentine.

Lower premolars.—Only 1 P_4 has been identified (Fig. 2*M*). The parastriid, mesostriid, and hypostriid are present, but only the mesostriid and hypostriid persist to the base of the tooth. The parastriid is open for 9.2 mm. down the side of the tooth. At this point the parastriid closes off and a parafossettid would be formed as wear progressed. The first anterior loph is inflated lingually.

as is the second anterior loph. The median loph is inflated labially, while the posterior loph is crescentic, concave anteriorly.

The paraflexid is in the shape of a crescent and is concave anteriorly. The termination is flat and does not abut tightly to the labial wall enamel.

The mesoflexid is directed anterolabially to a flat termination. The termination is separated from the enamel of the labial tooth wall by a tract of dentine. This situation exists both at the occlusal surface and the base of the tooth.

The hypoflexid extends posterolingually in a sinuous manner. The termination of the hypoflexid is flat, but does not abut tightly against the wall enamel at the occlusal surface, although the abutment is tight at the base.

Lower molars.—Two lower molars have been examined (Fig. 2*N* and *O*). In an early stage of wear the parastriid is present, but it is very short. This tooth (Fig. 2*N*) has a hypofossettid. Only the mesostriid and hypostriid are persistent to the base of both teeth. The first anterior loph is constricted in the middle, and the second anterior loph is inflated lingually (Fig. 2*N*). The median loph is inflated labially. The posterior loph may be straight and inflated labially, or crescentic, concave anteriorly and inflated labially.

When present the paraflexid has a sinuous configuration and is directed labially. The termination of the paraflexid is rounded and separated from the wall of the tooth by dentine.

The mesoflexid trends anterolabially and has a rounded termination. At the occlusal surface, the termination of the mesoflexid does not abut tightly against the labial wall of the tooth. At the base of the tooth, however, the abutment is tight.

The hypoflexid extends posterolingually. The termination of the hypoflexid is flat and abuts tightly against the lingual tooth wall at the base of the tooth, but not at the occlusal surface.

Discussion.—*Dipoides rexroadensis* is the latest representative of the genus in North America. Its cheek teeth are larger than those of any other species of the genus. All specimens of *D. rexroadensis* were taken from Upper Pliocene deposits. The localities are given in the section on referred material.

The teeth are prismatic and hypsodont. On the basis of the present material the teeth of *Dipoides rexroadensis* show less variation than those of *D. wilsoni* or *Procastoroides sweeti*. The hypostria, mesostria, hypostriid, and mesostriid are present on, and persist to the base of, all adult cheek teeth. The parastria, metastria, parastriid, and metastriid are present on unworn or little-worn teeth. The parastriid is present for most of the height of P_4. The molars have an S-shaped pattern. The parastria, when present, is opposite the hypostria. The hypostria or hypostriid is never opposite the mesostria or mesostriid. The metastria is shorter than the parastria. Fossettes and fossettids are present in young individuals only. There is no indication of closure of the pulp cavities in old individuals, and the patterns of the teeth are similar to those of other species of *Dipoides* illustrated by Shotwell (1955).

The features given above fit well with the diagnosis of the genus as given by Shotwell (1955, p. 142). Its large size is the main reason for retaining the

species *rexroadensis* as being distinct. The paraflexus is commonly directed, or passes anterior to the hypoflexus in the Rexroad form. The mesoflexus of P^4–M^2 curves more posteriorly in *Dipoides rexroadensis* than in *D. wilsoni*, a condition which is most evident in P^4.

From the study of the material at hand it is evident that *Dipoides rexroadensis* is not the same animal as *D. wilsoni* or any other species of the genus. It is probable, however, that *D. rexroadensis* is a descendant of *D. wilsoni*. More definite ideas concerning the relationship of the Rexroad species to other species of *Dipoides* await the discovery of better fossil material.

ORDER RODENTIA

Family Castoridae

Procastoroides sweeti Barbour and Schultz

(Figs. 2*Q*–*T*, 3, and 4)

Procastoroides sweeti Barbour and Schultz, 1937, Am. Mus. Novitates, 942: 6, fig. 3.
Eocastoroides lanei Hibbard, 1938, Kans. Acad. Sci., Trans., 40 (1937): 244, fig. 2.
Procastoroides lanei (Hibbard), Hibbard, 1941, Kans. Acad. Sci., Trans., 44: 279, pl. II, fig. 1.
P. lanei (Hibbard), Hibbard and Riggs, 1949, Geol. Soc. Amer., Bull., 60: 836.
P. sweeti Barbour and Schultz, Hibbard, 1956, PMASAL, 41 (1955): 174.

There seems to be a great amount of variation shown by the teeth of this beaver from the Meade Basin. Many of these specimens were formerly referred to *Eocastoroides* or *Procastoroides lanei*, but I believe this material to be correctly assigned to *P. sweeti*. Characters found in *E. lanei*, i.e., narrow posterior transverse diameter of M_3, confluence of hypoflexus with labial side of P^4, have been found to be variable, and are also seen in specimens designated as *P. sweeti* from the Chicago Natural History Museum.

Referred material.—From the Sand Draw locality (Pleistocene), Brown County, Nebraska: CNHM P14974, right jaw with I, P_3–M_3; CNHM P15507, LP_4; CNHM P15508, RM^3; CNHM P26165, right maxillary fragment, P^4–M^2.

The following localities are in Meade County, Kansas: 1, 2, 22, 3, and UM-K3-53. From locality 1 (Pleistocene) in the SW¼ Sec. 15, T. 33 S., R. 29 W: KUMNH 3843, fragmentary left jaw with M_2 and M_3; KUMNH 4577, right maxillary fragment with P^4–M^3; KUMNH 7301, RM_3.

Recovered from locality 2 (Upper Pliocene) in the NW¼ Sec. 22, T. 33 S., R. 29 W: KUMNH 3938, RM_3; KUMNH 3939, RM^3; KUMNH 4273, right upper molar; KUMNH 5967, LM_3.

KUMNH 6847, LM_3 was collected at locality 22 in the NW¼ Sec. 36, T. 34 S., R. 30 W.

The specimens from locality 3, in the SW¼ Sec. 22, T. 33 S., R. 29 W., at the University of Kansas Museum of Natural History are: KUMNH 7403, right jaw with P_4–M_2; KUMNH 5189, Rp^4. The following specimens from locality

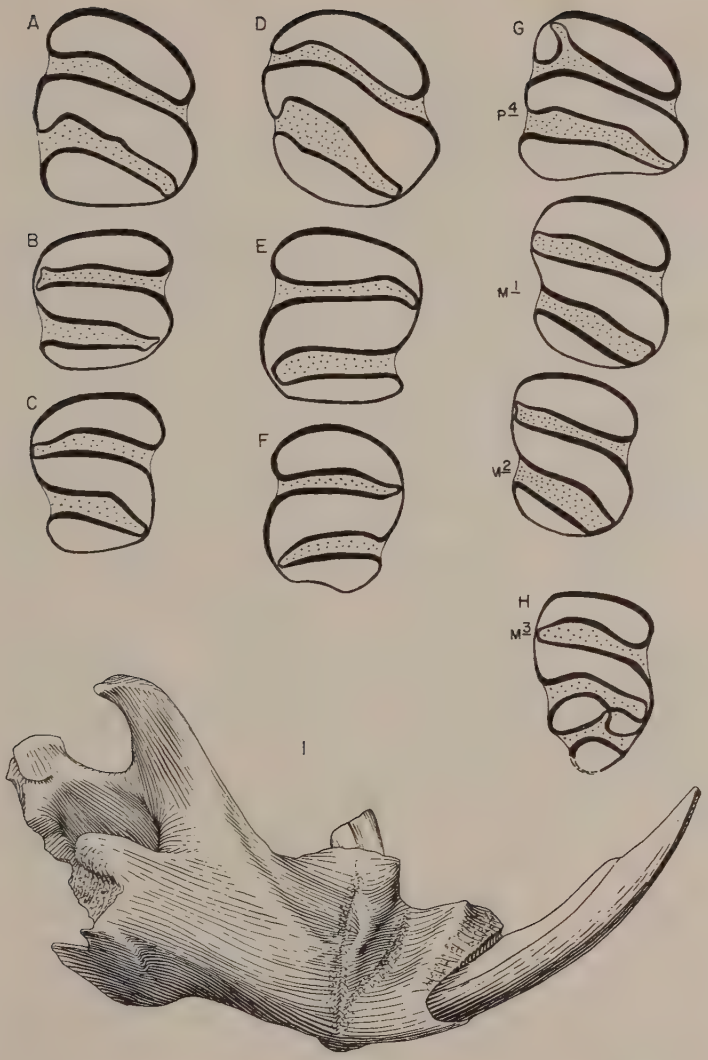

FIG. 3. *Procastoroides sweeti*. *A–F*, UMMP 41152; *A*, RP^4; *B*, RM^1; *C*, RM^2; *D*, RP^4; *E*, LM^1; *F*, LM^1; *G*, CNHM P26165, right maxillary fragment with P^4–M^2; *H*, CNHM P15508, RM^3. All ×-2. *I*, UMMP 42315, right jaw. ×-½.

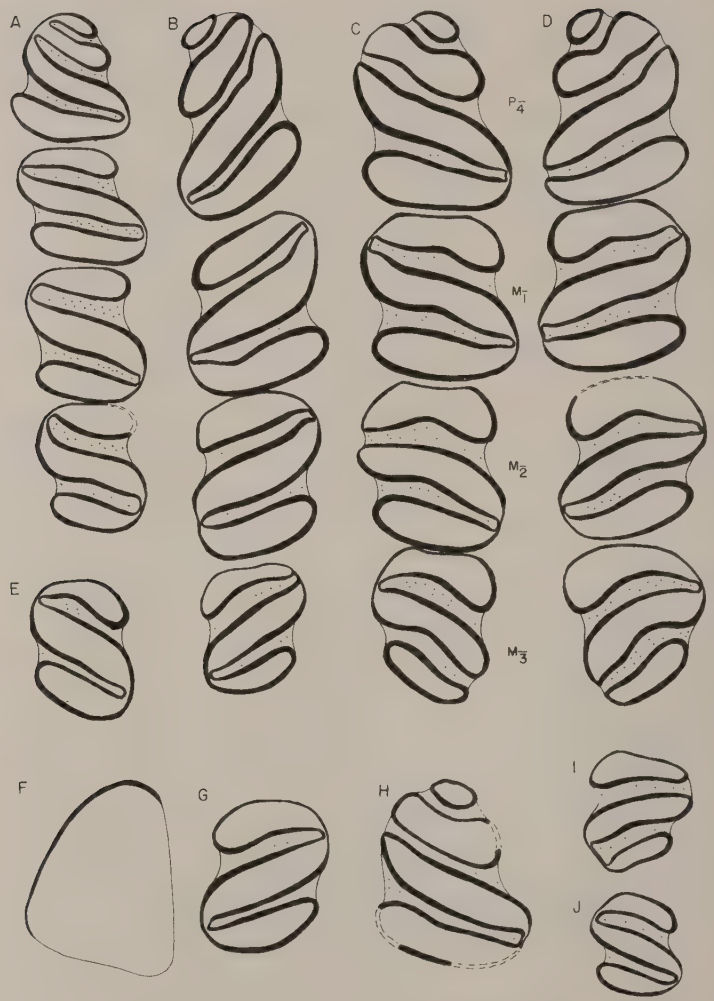

FIG. 4. *Procastoroides sweeti*, lower molars. *A*, UMMP, 26383, $LP_{\overline{4}}$–$M_{\overline{3}}$; *B*, UMMP 31295, $RP_{\overline{4}}$–$M_{\overline{3}}$; *C* and *D*, UMMP 31294, associated left (*C*) and right (*D*) dentitions, P_4–M_3; *E*, KUMNH 6847, RM_3; *F*, UMMP 41151, left lower incisor, cross-section; *G*, UMMP 41152, $LM_{\overline{1}}$; *H*, CNHM P15507, LP_4; *I*, KUMNH 7301, RM_3; *J*, KUMNH 5967, LM_3. All ×-2.

3 are in the collections of The University of Michigan Museum of Paleontology: UMMP 26383, associated left lower series, $P_{\bar{4}}$-$M_{\bar{3}}$; UMMP 29153, $RM^{2?}$ and $RM_{\bar{3}}$; UMMP 29645, left jaw with $P_{\bar{3}}$–$M_{\bar{3}}$; UMMP 31293, right jaw with incisor and $M_{\bar{3}}$; No. 31294, associated right and left jaws, I, $P_{\bar{4}}$–$M_{\bar{3}}$; UMMP 38419, left upper and lower incisor; UMMP 41152, two RP^4's, seven M^1's or M^2's, left and right $P_{\bar{4}}$, one $M_{\bar{1}}$?, right and left $M_{\bar{3}}$.

The remaining specimens were collected at locality UM-K3-53 in the $SW^1/_4$, $SW^1/_4$ Sec. 33, T. 33 S., R. 29 W: KUMNH 10293, $RP_{\bar{4}}$; UMMP 35070, right upper incisor, UMMP 41290, RM^3 and LM^2; UMMP 42314, $LP_{\bar{4}}$, $RM_{\bar{1}}$, and right upper incisor; UMMP 42315, right jaw with I and $P_{\bar{4}}$.

Upper premolar (Fig. 3*A*, *D*, and *G*).—Only 5 P^4's have been recovered. The P^4 is the widest tooth, and the most curved, of the upper series. The curvature of the teeth decreases progressively from P^4–M^3. The hypostria and mesostria are present on and persist to the base of all teeth. The anterior loph is crescentic, convex anteriorly. The median loph is either similar to the anterior loph or sinuous. The posterior loph is inflated labially.

The hypoflexus trends generally anterolabially to about the labial third of the tooth, at which point the trend becomes posterolabial. In all teeth examined, the hypoflexus extends through the labial side, the cement breaks through the termination, and a stria is formed. This separates the anterior loph from the rest of the tooth.

The mesoflexus trends posterolingually to a flat termination which abuts tightly and is associated with a pseudostria.

Upper first and second molar.—M^1 and M^2 are represented by 10 teeth, 6 of which are shown in Fig. 3*B*, *C*, *E*, *F*, and *G*. The hypostria and mesostria are present in and persist to the base of all teeth. The pattern is S-shaped. M^1 and M^2 are subequal in size, M^1 being the larger. The anterior loph is commonly crescentic, convex anteriorly, and inflated lingually. It may also be flat and uninflated. The median loph is usually bent posteriorly in the lingual part (Fig. 3*E*). The posterior loph is inflated labially and directed slightly anterolabially.

The hypoflexus usually passes anterolabially to a flat termination. One specimen, however, has a narrowed termination. The termination of the hypoflexus abuts tightly against the enamel of the labial wall in all but 4 teeth. Pseudostria occur on 4 other teeth.

The mesoflexus trends posterolingually to a flat termination which abuts tightly on the posterolingual tooth wall, and is associated with a pseudostria.

Upper third molar.—There are 4 M^3's, 3 of which are shown (Fig. 2*Q*, *T*, and 3*H*). The hypostria, mesostria, and metastria are present, and persist to the base of all of these teeth. The lophs are crescentic or chevrons and inflated or uninflated.

The hypoflexus trends, in various ways, more or less labially. Its termination is narrowed or flat. In 1 tooth the cement of the hypoflexus extends through the termination, and a stria is formed. This separates the anterior loph from the rest of the tooth. Pseudostria are associated with the termination of the hypoflexus in 2 teeth.

The mesoflexus passes, as a crescent or chevron, posterolingually. The termination of the mesoflexus is flat on all teeth. Pseudostria are found on 3 of the 4 M^3's.

The metaflexus is generally crescentic, convex anteriorly, although in 1 tooth (Fig. 3*H*), it is crescentic, concave anteriorly. The termination of the mesoflexus is narrowed. Note Fig. 3*H*, where the first posterior loph is constricted in the middle. At the base of this tooth 2 discrete circles of enamel have been formed.

Lower premolar (Fig. 2*S*, 4*A–D*, *H*).—Thirteen $P_{\bar{4}}$'s have been collected. The parastriid, mesostriid, and hypostriid are present on and extend to the base of all lower premolars. The first anterior loph is usually lenticular or tear-shaped (Fig. 4*A*). Where that loph is completely separated from the rest of the tooth, it is ovate (Fig. 1*S*). The second anterior loph is usually inflated lingually, but it may also be crescentic, concave anteriorly (Fig. 4*C* and *D*). The median loph may be smoothly crescentic, concave anteriorly (Fig. 4*A*), but it is more commonly directed anterolabially with a rather abrupt bend in the labial third (Fig. 4*C* and *D*). The posterior loph is usually inflated labially.

The paraflexid extends anterolabially, and in 4 teeth the cement breaks through the labial enamel, forming a striid on that side. Pseudostriids are associated with the termination of the paraflexid in all but 3 teeth, 1 of which, UMMP 26383 (Fig. 4*A*), appears to be that of a young individual. In this tooth the termination abuts tightly at the base of the tooth, and a pseudostriid appears only on the lower one-fourth. In all lower premolars the termination of the paraflexid with the labial wall of the tooth is flat.

The mesoflexid trends anterolabially. In 4 teeth the cement associated with it extends through the labial enamel and forms a striid on that side (Fig. 4*B-D*, and *H*). The termination of the mesoflexid with the labial tooth wall is flat in all specimens and abuts tightly against that wall in all but 1 tooth (Fig. 4*A*). Like the paraflexid, the termination of the mesoflexid of this tooth (UMMP 26383) abuts tightly at the base. A pseudostriid is formed here by the abutment of the termination of the mesoflexid in only the lower one-fourth of the tooth. In all other teeth the pseudostriid is associated with the termination of the mesoflexid for the full height of the tooth.

The hypoflexid trends posterolingually and may break through the lingual tooth wall (Fig. 4*D*). Other teeth have a definite tract of dentine separating the termination of the hypoflexid from the lingual wall of the tooth. The termination is rounded in UMMP 26383 (Fig. 4*A*) and flat in UMMP No. 31295 (Fig. 4*B*). In the former, the termination is flat and abuts tightly against the lingual tooth wall at the base.

Lower first and second molar (Fig. 4*A–D* and *G*).—There are 21 of these teeth. $M_{\bar{1}}$ and $M_{\bar{2}}$ are subequal in size, $M_{\bar{1}}$ being the larger. The pattern is S-shaped since only the mesostriid and hypostriid are present on and persist to the base of all of these molars. Pseudostriids are found on 8 teeth. The anterior loph is either inflated and crescentic, convex anteriorly (Fig. 4*C*, *D*, and *G*), inflated and straight (Fig. 4*B*) or uninflated and straight, in an anterolabial direction. The median loph trends anterolabially and is usually bent anteriorly on the labial side (Fig. 4*B–D*). It may be straight and slightly inflated (Fig. 4*G*) or straight and uninflated (Fig. 4*A*). The posterior loph is either crescentic, concave anteriorly and inflated labially (Fig. 4*D*, $M_{\bar{2}}$), or straight, in an anterolabial direction, and inflated labially (Fig. 4*C*, $M_{\bar{2}}$).

The mesoflexid trends anterolabially. The terminations are flat and abutnents of the terminations tight in all but 1 tooth. This tooth has a definite tract of dentine between the rounded termination and the labial wall enamel. $M_{\bar{3}}$ of Fig. 4*C* has a mesoflexid in which the cement breaks through the labial enamel, completely separating the anterior loph from the rest of the tooth.

The hypoflexid trends posterolingually. The termination of the hypoflexid is flat in all but 3 teeth, 2 of which are shown in Fig. 4*B*, $M_{\bar{3}}$, and 4*C*, $M_{\bar{1}}$. Pseudostriids are found on 11 teeth. The termination of the hypoflexid does not abut tightly against the lingual tooth wall in 2 specimens.

Lower third molar.—Thirteen $M_{\bar{3}}$'s were available for study, 7 of which are shown in Fig. 4*A–E*, *I*, and *J*. The teeth are short, with a height of 10–20 mm. The tooth is generally straight. The mesostriid and hypostriid are present on and persist to the base of all teeth. The occlusal pattern is S-shaped except when the cement of the hypoflexid extends through the labial and lingual enamel and separates the posterior loph from the rest of the tooth. The anterior loph is inflated lingually and directed anterolabially (Fig. 4*A*), or crescentic, convex anteriorly. The median loph is crescentic, convex anteriorly (Fig. 4*C* and *D*), or inflated and directed anterolabially (Fig. 4*J*). The posterior loph is often directed more anteriorly than the others and inflated labially (Fig. 4*C*, *D* and *J*). It may also parallel the trend of the median loph (Fig. 4*E*).

The mesoflexid passes anterolabially to terminate on the labial side of the tooth. All terminations abut tightly except in 3 teeth, 2 of which are shown in Fig. 4*E* and *J*. In these 3 specimens the terminations are rounded and have no associated pseudostriids. One of them (Fig. 4*A*) has a rounded termination at the occlusal surface, but a flat one at the base of the tooth and no pseudostriid. Pseudostriids are associated with the abutments of the terminations of 5 teeth.

The hypoflexid passes posterolingually and terminates on the lingual side of the tooth. In 3 specimens the cement extends completely across the tooth from labial to lingual side. This isolates the posterior loph in 2 teeth (Fig. 4*C* and *D*). The termination of the hypoflexid is flat and abuts tightly against the labial wall in all specimens, with the exception of the 2 teeth. In these 2, the termination is rounded and separated from the lingual wall of the tooth by a tract of dentine. In Fig. 4*E* the termination is flattened and abuts tightly at the base of the tooth. Pseudostriids are found on 3 teeth.

Incisors.—The upper incisor is larger in width (15.7–19.2 mm.) and depth (13.8–15.4 mm.) than the lower. None of the upper incisors was directly associated with material that can definitely be assigned to the genus *Procastoroides*. No other large upper incisors have been collected from these deposits, however, so that it seems reasonable to assign these teeth to that genus. All 6 upper incisors examined have a groove on the internal surface (Fig. 2*R*) which is labial to the midline of the tooth and may be either very faint or very pronounced. In 3 teeth there is also a groove on the outer (enamel) surface at, or labial to, the midline (Fig. 2*R*). Like the internal groove, the outer one can be either shallow or deep. In 1 specimen, UMMP 35070, the groove is double. This tooth is the widest and has the most pronounced outside groove of the 6 incisors. If it is correctly assigned to *Procastoroides* it may represent a different species, but the incisor is not directly associated with any other definitive material.

TABLE II

MEASUREMENTS* OF TEETH OF *Procastoroides sweeti*

	Mean Length	Mean Width	Range of Length	Range of Width	No. of Specimens
P^4	11.3	10.7	10.5–12.6	9.5–11.8	5
M^1	9.3	8.7	8.0–10.5	8.0–9.3	2
M^2	8.8	8.3	7.5–10.0	7.5–9.0	2
M^3	9.3	6.9	8.0–11.1	6.0–7.5	4
P_4	12.3	9.0	9.2–14.2	8.3–11.3	13
M_1	11.4	9.3	10.2–13.0	7.6–10.2	7
M_2	11.1	8.9	9.5–12.5	7.8–10.0	9
M_3	9.8	8.2	9.0–11.0	6.6–9.2	5

* In millimeters. See Fig. 2*P* for illustration of method.

There is now no valid basis for proposing a new species name for this specimen, but its differences are interesting and may prove to be significant when more material is collected.

The lower incisor is triangular in cross section (Fig. 4*F*), bears no grooves on the outer or inner surfaces, and has no crinkling of the enamel. Its form and configuration seem to be stable. The lower incisor is nearly as wide as deep (Tab. III), is twisted labially in the posterior part, and passes directly beneath P_4, and lingual to M_1 and M_2. In KUMNH 3843 the base of M_1 rests wholly on the incisor, whereas in 3 other jaws the incisor covers only the lingual part of the base of M_1. This is similar to the condition in *Castoroides* (UMMP 3109).

Lower jaw.—None of the 9 jaws or jaw fragments is complete, and only 4 have P_4–M_3. That of CNHM P14974 is in poor condition, but the jaw is interesting for its small size. The length of the occlusal surface (Tab. III) is much less than that of the other 3, but the tooth pattern is completely comparible with that of other rami. This mandible is quite probably that of a young adult. Some of the teeth of UMMP 31294, associated right and left jaws with complete dentitions, represent the most advanced stages of development with respect to complete separation of the lophs by tracts of cement (Fig. 4*C* and *D*). Most of the mandibles are rugose and have a well developed masseteric ridge which is, in general, proportionately more developed than in *Castoroides* (UMMP 3109). The capsular process on UMMP 42315 is slightly more pronounced than that of *Castoroides*. The articulating surface of the posterior condyle of UMMP 31294 and 42315 is less broad laterally than that of *Castoroides*. KUMNH 3843 is fragmentary and contains only M_2 and M_3 (Hibbard, 1938, fig. 2). No measurements could be taken on this specimen. CNHM P26165, with P_4–M_3, was available for study, but it was not sufficiently complete. No measurements could be taken on it. Measurements involving the tip of the incisor were not used because of the possibility of slippage of the incisor in the alveolus. Such measure-

TABLE III

MEASUREMENTS* ON JAWS OF *Procastoroides sweeti*

Specimen No.	Length, P_4–M_3, at Occlusal Surface	Depth of Jaw below Anterior Edge, P_4	Length, Posterior Condyle to Tip of P_4	Width of Incisor	Depth of Incisor
UMMP 31294 (right)	51			10.0	11.2
UMMP 31294 (left)	50	46	90	10.0	11.2
UMMP 31295	50	44			
UMMP 42315		44	90	12.0	12.8
UMMP 31293		43		9.6	10.6
UMMP 29645		46			
KUMNH 7403		44			
CNHM P14974	41	40			

* In millimeters.

ments as could be taken are presented in Table III. The figures obtained seem to correspond well to those published by Barbour and Schultz (1937, p. 7).

Diagnosis.—The cheek teeth are strongly hyposodont and prismatic, with complete hypostria, mesostria, hypostriid, and mesostriid. P_4 has a complete parastriid, M^2 a complete metastria. There is no tendency for the base of the teeth to close with age. Pseudostria and pseudostriid are often well developed in association with the tight abutment of terminations. There is a tendency for the lophs to become isolated from each other by tracts of cement. This is most well developed in the P_4, but occurs to varying degrees in all other teeth. Upper and lower M1 and M2 most commonly display the S pattern. No fossettes or fossettids were found on the teeth examined. The dorsal surface of the lower incisor is twisted labially posteriorly, passes below P_4, lingual to M_1 and M_2, and usually covers only the lingual part of the base of M_3. The depth of the lower incisor is proportionately less than that of *Castoroides*. The upper incisor is larger than the lower, possesses grooves on the internal, and variably, on the outer, enamel surface. There is no crenulation of enamel on either upper or lower incisor. The masseteric ridge is proportionately more developed, the capsular process relatively more pronounced than in *Castoroides*. Dental foramen usually better developed than the mental.

Discussion.—This is a large beaver, larger than *Dipoides* or the modern beaver, but about two thirds the size of *Castoroides*. There is, in *Procastoroides*, a tremendous amount of variation indicated by the teeth, with a tendency toward separation of the lophs by tracts of cement. There is no observable trend toward an increase in size through time. The Pleistocene forms studied are about the same size as, or smaller than, the Pliocene forms. In the material at hand, there are no characters by which one age group can be separated from the other. As far as can be seen, there is no valid reason for not retaining the

same species name for the forms of both ages. The group is apparently an end line; it exhibits characters which are too specialized to be transitional to the modern beaver. *Procastoroides* probably developed independently the tendency toward the complete separation of lophs by tracts of cement. It is interesting to note, in contrast with the variation in the cheek teeth and the variable presence and position of grooves in the outer surface of the upper incisor, the apparent stability of the form and configuration of the lower incisor. If *Procastoroides* were the ancestor of *Castoroides*, whose earliest fossil record is Kansan, why is there no observed trend toward crenulation of the incisor enamel also?

Although the parastriid is long, and variably occurs for the complete height of the tooth in Dipoides, there is no species of that genus in which a persistent parastriid is a consistent feature. I do not believe that *Procastoroides* arose directly from *Dipoides*, but probably from some stock near the *Eucastor-Dipoides* transition in the lower or early middle Pliocene.

ORDER PROBOSCIDEA

Family Gomphotheriidae

Stegomastodon rexroadensis Woodburne sp. nov.

(Pls. II–IV)

Stegomastodon successor (Cope), Hibbard and Riggs, 1949, Geol. Soc. Amer., Bull., 60: 838.

Holotype.—UMMP 41207, associated right and left upper and lower M2 and M3 collected from locality 3.

Paratypes.—Additional remains collected at locality 3 are: KUMNH 4637, fragmentary right jaw with M_{1} and M_{2}; KUMNH 4638, right and left M^{2}; KUMNH 4640, right and left upper and lower M3; UMMP 29996, RM_{2}, at locality UM-K3-53; UMMP 28125, RM_{3}; UMMP 33366, right and left jaw with M_{3}; UMMP 35099, RM^{3}; and UMMP 40245, RM^{3}.

Horizon.—All specimens were taken from beds of the upper Pliocene Rexroad formation. Locality 3 is in the W½, SW¼ Sec. 22, T. 33 S., R. 28 W., Rexroad Ranch, and locality UM-K3-53 is in the SW¼, SW¼ Sec. 33, T. 33 S., R. 29 W., Wendell Fox Pasture, Meade County, Kansas.

Diagnosis.—A short-jawed mastodont whose teeth show a simple, primitive trefoiling. Enamel is not present on adult tusks. No double trefoils are developed on the lower teeth. Trefoil spurs are simple. It is possible that double trefoils would form as wear progressed on the proto- and metaloph of M^{3}. The teeth and jaws are smaller than is usual for *Stegomastodon mirificus* (Leidy) or *Haplomastodon waringi* (Holland). Upper and lower M3 of *S. rexroadensis* are the same size as those teeth of *S. primitivus* Osborn, but the jaw of *S. rexroadensis* is smaller. The intermediate molars of *S. rexroadensis* are less ptychodont than those of *S. mirificus* and *S. primitivus*, and probably *H. waringi*. The third molars of the Rexroad species have 5+ lophs. The ptychodonty of M_{3} of *S. rexroadensis* equals that of M_{2}.

Description of holotype.—The terminology used is that set forth by Osborn (1936) and clarified by Savage (1955, p. 51). Measurements of these and other teeth are included in Table IV.

The teeth of the holotype (Pls. II and III) are those of a mature individual; the tetartoloph and tetartolophid of M3 had begun to be affected by wear. M^2 has 2 anterior roots and exhibits slight centroversion of the lophs, while M_2 has but one anterior root, and the lophids are proverted internally. The 3 lophs and lophids of upper and lower M2 are worn nearly to the cingulum, but that part of the enamel remaining shows no indication of ptychodonty (plication).

TABLE IV

MEASUREMENTS* OF TEETH OF *Stegomastodon rexroadensis*

Museum No.	Tooth	Crown Length	Crown Width	Approx. Index	Lophs or Lophids	Width of Pentaloph or Pentalophid of M3	Stage of Wear
UMMP 41207	RM^2	98	72	73	3+		Mature
"	LM^2	99	71	71	3+		Mature
"	RM^3	193	82	42	5+	65	Mature
"	LM^3	192	83	43	5½	63	Mature
KUMNH 4640	RM^2	171+	80	?	5+	51	Late mature
"	LM^3	183	76	41	5+	52	Late mature
KUMNH 4638	RM^3	188	81	43	5+	52	Mature
"	LM^3	191	84	44	5+	59	Mature
UMMP 40245	RM^3	190	83	44	5+	53	Young adult
UMMP 35099	RM^3	225	100	40	5½	77	Mature
KUMNH 4637	RM_1	90	60	66	3		Young adult
"	RM_2	123	72	58	3+		Young adult
UMMP 29996	RM_2	110	74	67	3		Young adult
UMMP 41207	RM_2	98	69	70	3		Mature
"	LM_2	97	69	70	3		Mature
"	RM_3	204	89	44	5+	67	Mature
"	LM_3	208	87	42	5½	73	Mature
KUMNH 4640	RM_3	209	81	39	5+	78	Mature
"	LM_3	192+	81	?	5½	62	Mature
UMMP 33366	RM_3	206	79	38	5½	66	Old age
"	RM_3	204	77	38	5½	67	Old age
UMMP 28125	RM_3	196	76	39	5½	70	Young adult

* In millimeters. Index $= \left(\frac{\text{width}}{\text{length}} \times 100\right)$

There are no double trefoils present at this stage of wear, and no accessory conules or conulids are apparent.

Like M^2, M^3 has 2 anterior roots; the lophs are centroverted. The lophids of M_3 show internal proversion, and there is only 1 anterior root. The occlusal surface of M_3 has begun to wear concave dorsally, while the outline of that of M^3 is concave ventrally. The third molars are well formed, 5+ lophs are present on the M^3, and an equal number of lophids are found on M_3. The proprotoloph and pro-protolophid are absent. The dental pattern is best, but not fully, developed on the protoloph and protolophid. The pattern of upper and lower M3 shows primitive, incipient, double trefoils.

In M^3 the configuration of the lophs is such that the development of double trefoils is possible on the proto- and metaloph. With wear, entotrefoils would develop on the tritiloph, and perhaps on the tetratoloph as well. The tritiloph would also bear either the anterior or posterior spur of an ectotrefoil, but not both. No trefoils would form on the penta- and hexaloph. Accessory ectoconules are present anterior and posterior to the tritiloph.

No complete double trefoils will form on M_3. Ectotrefoils will develop on the proto-, meta-, triti-, and possibly the tetartolophid. The protolophid has the posterior spur of an entotrefoil. The meta-, triti-, and tetartolophid each have an anterior spur of an entotrefoil. No trefoils will form on the pentalophid or hexalophid. An accessory entoconulid is present between the proto- and metalophid. Anterior and posterior spurs of trefoils in both upper and lower teeth are simple. Neither the hexaloph of M^3 nor hexalophid of M_3 is well developed, and it is not possible to determine with certainty the number of elements of which they are composed. In all cases the enamel pattern is simple.

Segments of tusk material, totaling at least 18 inches in length, were found associated with the teeth of the holotype. None of these segments was collected because the plates of the tusk fell apart quite readily. There was, however, no evidence of enamel found, either with the segments or as loose plates in the surrounding matrix. On the basis of the above features, the number of lophs and lophids, the nature of the trefoils, and the absence of tusk enamel in the adult, the holotype is placed in the genus *Stegomastodon*. It is noted further that the animal represented by this material seems to be a primitive one, in the stegomastodont line, and may be closely related to *Haplomastodon* as well. These ideas will be discussed in more detail below.

Description of paratypes.—The ptychodonty of upper and lower M3 is neither more nor less complex than that of upper and lower M1 or M2. The enamel of all teeth is simple, not plicated. Trefoil spurs are simple. All stages of wear from young adult to old age are represented by the third molars. The dental variation of this species is slight, and most teeth are comparable to those of the holotype. Measurements taken from the teeth are compiled in Table IV.

First lower molar.—Only 1 first molar is available for study. It is an M_1 and is associated with M_2 in the fragmentary jaw, KUMNH 4637 (Pl. IV, Fig. 2). It is shorter than M_1 of *Haplomastodon waringi* (Holland) (see Simpson and de Paula Couto, 1957, tab. 6), but its width closely approximates the mean width of that tooth in *H. waringi*. The enamel of M_1 of *H. waringi* (Simpson and de Paula Couto, 1957, pls. 4, 7, 8) is more plicated than that of *Stegomas-*

todon rexroadensis. The enamel of M_1 of *S. mirificus* (Leidy) (see Savage, 1955, pl. 2) is also more plicated than that of *S. rexroadensis*. There is no evidence of accessory conulids on M_1 in the Rexroad species.

Second upper and lower molars.—The lophs of the upper and lower M2's of all specimens except KUMNH 4637 and UMMP 29996 (Pl. IV) are worn nearly to the cingulum. When the enamel of M2 is nearly worn away, its anterior end becomes abraded and shortened, giving a false impression of the length. This is the case with M2's of the holotype. The configuration of these teeth has been mentioned above. It can be seen from Table IV that M^2 is shorter and wider than M_2. The relatively unworn M_2's of specimen KUMNH 4637 and UMMP 29996 have no accessory conulids, and ectotrefoils are present. The protolophid would also form a posterior spur of an entotrefoil. The meta- and tritilophid would each develop an anterior spur of an entotrefoil. Wear is not yet extensive on either the anterior or the posterior end of these teeth, so it is believed that the measurements obtained here represent better lengths of M_2. The widths of the upper and lower M2's of the Rexroad species fall within the range of the widths of M2 of *Haplomastodon waringi* given by Simpson and de Paula Couto (1957, Tab. 6). Only the length of M_2 KUMNH 4637 is compatible with the figure for *H. waringi*. All other M2's of *Stegomastodon rexroadensis* are shorter. M^2's of the Rexroad sample are as wide as, but shorter than, those of *S. mirificus* from Cita Canyon, Texas (Savage, 1955, Tab. 4). M_2's of *S. mirificus* from that locality are wider and longer than those of the Rexroad species. Savage (1955, p. 59) notes that "M_2 is more ptychodont than M_3 in the Cita Canyon materials." This is not the case in the Rexroad species, but rather ptychodonty is the same for M_3 as for M_2. M2's of *S. mirificus* (Savage, 1955, pl. 2) are more ptychodont than those of *S. rexroadensis*.

Third upper and lower molars (Pls. II and III).—The enamel pattern of these teeth is directly comparable to that of the holotype. UMMP 28125 and UMMP 40245 are in an early stage of wear and show well the configuration of the unworn lophs and lophids. Even at this stage of wear the pro-protoloph and pro-protolophid are not well defined and were probably worn away earlier by M2. In only 2 teeth, UMMP 33366, is the enamel worn nearly away.

UMMP 35099 is large, but it is split and fractured in many places. These openings are filled with matrix, so that the apparent large size may be misleading. On the basis of centroversion of its lophs, this tooth is a RM^3. It is in a late mature stage of wear and is significant in that no double trefoils are evident. Double trefoils would probably not develop at any stage of wear in this tooth. The right and left M^3's, KUMNH 4638, are in a mature stage of wear; the pro-protoloph is absent. Ectotrefoils will not form on any of the lophs. The protoloph has the posterior spur of an ectotrefoil, but not the anterior; the metaloph has the anterior spur, but not the posterior. The other lophs are so constructed that none would have even the beginning of an ectotrefoil pattern. M^3's of KUMNH 4640 are in a late mature stage of wear, and it is not possible to determine the complete pattern clearly. Ectotrefoils are developed on the proto-, meta-, and possibly the tritiloph. A double trefoil is present on the protoloph of LM^3. On other lophs of these teeth, incipient double trefoils are variably present, but none is well formed. Accessory conules are variable in

their occurrence on M^3, but ectoconules are commonly found anterior and posterior to the metaloph.

M_3's of KUMNH 4640 are in a mature stage of wear and show no double trefoil development. Ectotrefoils are well formed on the first 3 lophids. On the tetartolophid, an ectotrefoil of sorts is present, but it is skewed. No trefoils would develop on the pentalophid. Entoconulids are most commonly situated anterior to the metalophid. While M_3's of UMMP 33366 are so worn that there is almost no enamel remaining, their size fits well with that of M_3's of the holotype. The significance of these worn teeth lies in the fact that they sit in associated right and left jaws. The remaining M_3's in the Rexroad sample have been mentioned above.

The size of upper and lower M3 in *Stegomastodon rexroadensis* falls into the lower size limit of those of *S. mirificus* from Cita Canyon (Savage, 1955, tab. 2 and 3), and fairly close to the average upper and lower M3 of *Haplomastodon waringi*, as compiled by Simpson and de Paula Couto (1957, tab. 6). The measurements for upper and lower M3 of *S. primitivus* (Osborn, 1936, p. 727) are contained within those given for these teeth of *S. rexroadensis* in Table IV. From Fig. 675 of Osborn (1936, p. 726) it seems that double trefoils would develop on the first 2 lophs of M^3 in *S. primitivus*, but that none would form on M_3. M^3 of *S. primitivus* appears more complex, in the composition of the lophs, than that of the Rexroad species, but M_3 of *S. primitivus* is quite similar to that of *S. rexroadensis*. One of the main differences between *S. primitivus* and *S. rexroadensis* lies in the more complicated character of the enamel in upper and lower M2 of *S. primitivus*. This form also has a very large jaw in comparison with its tooth size (Savage, 1955, p. 66).

Lower jaw.—UMMP 33366 represents the only measurable set of jaws in the Rexroad collection. The jaws contain right and left M_3's whose sizes are close to those of the holotype. This right and left mandible was compared with associated right and left jaws of *Stegomastodon mirificus*, UMMP 26363 and 24314, from the Pleistocene of Kansas. The symphyseal length of the Rexroad specimen is 115 mm., while those of the Pleistocene forms are 115 mm. and 107 mm., respectively. In the Rexroad species, the distance from the tip of the jaw to the anterior border of the posterior mental foramen is 180 mm. The same measurement for *S. mirificus* is 150–175 mm. (Savage, 1955, Tab. 7). The average length of M_3 of *S. rexroadensis* can be shown to be 85 per cent of the average length of M_3 in specimens of *S. mirificus*. It can also be demonstrated that the length of the pretooth part of the jaw of *S. rexroadensis* is the same as, or slightly larger than, that part of the jaw of *S. mirificus*. Thus, the pretooth part of the jaw of *S. rexroadensis* is longer than that which would be expected from the size of its teeth. However, the shape of that part of the jaw of the Rexroad species is nearly identical to that of *S. mirificus*. The pretooth part of the jaw of *Haplomastodon waringi* is more rhynchorostrine than that of either *S. mirificus* or *S. rexroadensis*.

Discussion.—Hibbard and Riggs (1949, p. 838) assigned KUMNH 4640 to *Stegomastodon successor* (Cope), but Savage (1955, p. 64) is of the opinion that the features of the type of this species are contained within the Cita Canyon material of *S. mirificus*. I believe that the Rexroad material is different from

TABLE V

MEAN INDICES OF MOLARS*

Tooth	*H. waringi*	*S. primitivus*	*S. mirificus*	*S. rexroadensis*
M^2	61		62	72
M_2	56		62	66
M^3	45	41	38	42
M_3	38	42	37	40

* Compiled from Simpson and de Paula Couto (1957), Osborn (1936), Savage (1955), and Table IV of this report.

the other species of *Stegomastodon* and have accordingly given it a new species name.

Since a larger molar index indicates that a tooth is wide relative to its length, a general comparison of tooth proportions may be made between various forms. It can be seen from Table V that upper and lower M2's of *Stegomastodon rexroadensis* are relatively wider than those of *S. mirificus* or *Haplomastodon waringi*. M^3 of the Rexroad species is intermediate in relative width between those teeth of *H. waringi* and *S. mirificus*, but has nearly the proportions of M^3 of *S. primitivus*. On the other hand, M_3's of *H. waringi* and *S. mirificus* are relatively narrower than those of *S. rexroadensis* and *S. primitivus*.

When these points are considered with the close correspondence in pattern of upper and lower M3 of *Stegomastodon primitivus* and *S. rexroadensis*, it appears that these 2 are more closely related than the Rexroad form is to either *S. mirificus* or *Haplomastodon waringi*.

In considering the features of *Stegomastodon primitivus*, Savage (1955, p. 66) noted that although the teeth of this form are small, 1 of the jaws referred to this species is nearly 100 mm. longer than any of the jaws of *S. mirificus* from Cita Canyon. Savage also mentiones that M^2 and M^3 of *S. primitivus* are as ptychodont as most of those teeth of the Cita Canyon and Blanco specimens. From this, it seems as though *S. primitivus* also possesses features which are typical of *S. mirificus*.

Savage (1955, p. 67) studied KUMNH 4637 and 4640; UMMP 28125 and 29996, and stated that "if all these specimens belong to one population, such a population is distinct from other brevirostrine gomphotheres and merits a new species name." From a study of the above and additional specimens I believe that Savage's statement is correct. The main feature which distinguishes *Stegomastodon rexroadensis* from other species of the genus is the simple configuration of the enamel in the first and second molars. The lack of plication in these teeth has been referred to by Savage (1955, p. 68) as a "simple gomphothere type of enamel folding." Savage compared the Rexroad materials mentioned above with specimens from Miñaca and Santa Ana de Babícara localities in Mexico. He believes that the specimens from the Mexican sites

closely resemble the Rexroad materials, and that, compared to these, the trefoils of the Cita-Blanco specimens are much more complex.

The teeth of *Haplomastodon waringi* are also less ptychodont than those of *Stegomastodon mirificus*. The Brazilian form apparently tends to develop, in some specimens, double trefoils on the proto- and metalophid of M_3, as well as on the protoloph and metaloph of M^3. The enamel of M_3 of *H. waringi*, while less ptychodont than that of *S. mirificus*, is more so than M_3 of *S. rexroadensis* (see Simpson and de Paula Couto, 1957, pls. 10 and 11). The trefoil spurs of these teeth of *H. waringi* also appear to be more complex than in similar specimens of *S. rexroadensis*. None of M^3's of the Rexroad species is composed of less than 5+ lophs, whereas many M^3's of *H. waringi* consist of only 5 lophs.

According to Simpson and de Paula Couto (1957, p. 163), the age of the deposits from which *Haplomastodon waringi* has been collected is fairly late Pleistocene or, in some cases, early Rexent, and "it is questionable, depending on decision as to the Pliocene-Pleistocene boundary, whether the mastodonts had yet reached South America in the earliest Pleistocene." On the other hand, Savage (1955, p. 69) proposes the idea that "the early haplomastodont stegomastodonts reached the South American continent at about the time of existence of the Rexroad, Miñaca, and Benson faunas, or slightly earlier." This view would put the mastodonts in South America by the Upper Pliocene. To my knowledge no record of mastodonts existing in South America at that time has been reported.

That the Rexroad species is related to *Haplomastodon waringi* is shown by the simple trefoiling in the enamel pattern of the intermediate molars, and the absence of enamel on the tusks in the adult stage. This relationship is noted by Savage, who states that "in animals of this character there appear to lie the structural annectants between earlier, rhynchorostrine gomphotheres and later, brevirostrine ptychodont stegomastodonts" (Savage, 1955, p. 68).

Concerning this, I believe that the pretooth part of the jaw is more rhynchorostrine in *Haplomastodon waringi* than in *Stegomastodon rexroadensis*, and that of the two, *H. waringi* is possibly closer to the rhynchorostrine complex (see Savage, 1955, fig. 8). The pretooth part of the jaw of *S. rexroadensis* is similar to that of *S. mirificus*.

In the area of the Rexroad fossil localities the fossiliferous deposits are overlain by about 50 feet of sediments. These contain massive caliches and, in one locality, the strata of the Bender local fauna. The Rexroad silts are overlain by the discontinuous sand and gravel of the basal Pleistocene. The discontinuous nature of this sand and gravel suggests that erosional forces, acting over a long interval, shaped deep valleys or gullies in the Rexroad deposits. These low areas were receptacles for the sand and gravel, but were so deep that the sediment-carrying streams did not completely fill them with the coarse material. Filling of the low areas occurred later, when the streams were carrying finer sediment. Prior to the next glacial stage, when little or no sediment was being deposited, agents of erosion again began to carve the topography. That the sand and gravel of the next glacial stage is widespread and continuous would tend to indicate that the erosional interval between the first 2 glacial

stages was not so great as that between the end of Rexroad time and the first stage of the Pleistocene.

The evidence suggests that there was a considerable amount of time available for dental alteration between the days of *Stegomastodon rexroadensis* and the appearance of *S. mirificus* or *S. primitivus* in the early Pleistocene. Savage (1955, p. 69) suggests that the Rexroad species "is phyletically primitive in the *Stegomastodon* line and is an early representative of this line in North America." If this is so, it would appear, from *S. primitivus*, that ptychodonty began to develop first in the upper molars. That M_3 of *S. primitivus* is nearly identical to those teeth of *S. rexroadensis*, even after the time lapse from the deposition of the Rexroad material to the early Pleistocene, seems to be a fairly reasonable indication of the affinity between the 2 forms. This, along with the nature of the pretooth part of the jaw, the presence of more than 5 lophs on on M^3, the greater tendency toward the development of double trefoils in M^3 rather than in M_3, and its closer geologic and geographic proximity to other species of *Stegomastodon* than to *Haplomastodon*, would indicate that *S. rexroadensis* is, in fact, a primitive member of the stegomastodont line, and is more closely related to *Stegomastodon* than to *Haplomastodon*.

Paleoecology

According to Hibbard (1941b, p. 101), the Rexroad fauna indicates a more moderate climate than that found at the present in southwestern Kansas. As originally described, the Rexroad fauna contained some Pleistocene fossils from Meade County locality 1. They were *Pliolemmus antiquus* Hibbard and *Pliopotamys meadensis* Hibbard, and carried northern connotations. It was pointed out by Hibbard (1941b, p. 101) that these forms probably belonged to a later fauna. Evidence was presented by Hibbard (1956, pp. 174–176) that *Pliolemmus* and *Pliopotamys* were members of the early Pleistocene faunas. It has been noted by Hibbard (1941b, p. 101) that if the genera mentioned above were excluded from the Rexroad fauna, the fauna would have southern and southwestern affinities, rather than northern. From the preceding discussion it seems as though the Rexroad fauna does, indeed, carry a southern connotation.

Of the forms discussed in this report, the beavers will be considered first. There is no direct evidence as to the habitat requirements of *Dipoides* and *Procastoroides*. The modern beaver occurs in continental North America, south to the Rio Grande (Hall and Kelson, 1959, map 321). It is found in aquatic situations, usually along streams, and feeds on willow, alder, birch, aspen, and other trees (Hall and Kelson, 1959, p. 542). While it cannot be assumed that

Dipoides and *Procastoroides* had requirements identical to those of the modern beaver, there is a definite implication of permanent water.

The teeth of *Stegomastodon* indicate browsing food habits which would require wooded areas, perhaps along the streams (Hibbard, 1941b, p. 99).

Further evidence of the ecologic situations mentioned above is given by the avian fauna. In his study of the birds of the Rexroad fauna, Wetmore (1944, p. 91) states that "Of the identified specimens more than one-half belong to aquatic species that live in and around marshes, streams and ponds. Remains of turkeys represent birds of wooded areas, while parrots, pigeons and quail are species of forests, or regions where thickets and groves grow amid plains, prairies or savannas. The passeriform birds may have lived in prairie land, in thickets or in forests."

Thus, it seems as though the Upper Pliocene climate of the Meade Basin, as shown by the Rexroad fossils, was considerably moister than that of the present. An indication of the Upper Pliocene temperatures is given by the large terrestrial tortoises which occurred at that time. Hibbard (1960, p.16) has noted that "The remains of these large tortoises [*Geochelone rexroadensis* (Oelrich), 1952] have been found in stream, artesian spring, and flood plain deposits of the Upper Pliocene, in Meade County, Kansas (elevation 2500–2600 feet). It is assumed that they lived in the region at a time when freezing conditions did not exist." From this it is evident that the annual temperature extremes were not as great when the Rexroad fauna existed as they are now.

Acknowledgments

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I am grateful to William Turnbull, Chicago Natural History Museum, and Robert W. Wilson, University of Kansas Museum of Natural History, for permission to study fossils under their care.

The field parties of the Museum of Paleontology, The University

of Michigan, contributed, during the summers of 1950–59, much effort in the collection of the fossil material. Appreciation is also expressed to Wendell B. Fox of Plains, Kansas, for granting permission to work on his land, where quarry UM-K3-53 is situated. He has long been interested in this work, and in the spring of 1955 recovered the associated right and left jaws of *Stegomastodon rexroadensis*, UMMP 33366, after they had been exposed by a flood.

I have prepared all the illustrations used in this report.

LITERATURE CITED

Barbour, Erwin H., and C. Bertrand Schultz. 1937. An Early Pleistocene Fauna from Nebraska. Am. Mus. Novitates, 942: 1–10, 4 figs.

Byrne, Frank E., and Thad G. McLaughlin. 1948. Geology and Ground-Water Resources of Seward County, Kansas. Kans. Geol. Surv., Bull., 69: 1–140, 12 pls., 9 figs., 10 tab.

Frye, John C. 1940. A Preliminary Report on the Water Supply of the Meade Artesian Basin, Meade County, Kansas. Kans. Geol. Surv., Bull., 35: 1–39, 5 pls., 7 figs., 3 tab.

—— and Claude W. Hibbard. 1941. Pliocene and Pleistocene Stratigraphy and Paleontology of the Meade Basin, Southwestern Kansas. Kans. Geol. Surv., Bull., 38: 389–424, 4 pls., 3 figs.

—— and Stuart L. Schoff. 1942. Deep-Seated Solution in the Meade Basin and Vicinity, Kansas and Oklahoma. Amer. Geophys. Union, Trans: 35–39, 3 figs.

Hall, E. Raymond, and Keith R. Kelson. 1959. The Mammals of North America. Ronald Press, New York. 1–1162, 553 figs., 500 maps.

Haworth, Erasmus. 1896. Local Deformation of Strata in Meade County, Kansas, and Adjoining Territory. Am. Jour. Sci., Ser. 4(2): 368–373, 1 map.

Hibbard, Claude W. 1938. An Upper Pliocene Fauna from Meade County, Kansas. Kans. Acad. Sci., Trans., 40 (1937): 5 pls., 2 figs.

—— 1941a. Mammals of the Rexroad Fauna from the Upper Pliocene of Southwestern Kansas. *Ibid.*, 44: 265–313, 4 pls.

—— 1941b. Paleoecology and Correlation of the Rexroad Fauna from the Upper Pliocene of Southwestern Kansas, as Indicated by the Mammals. Kans. Univ. Sci. Bull., 27 (Pt. 1, No. 6): 79–104.

—— 1949. Pliocene Saw Rock Canyon Fauna in Kansas. Univ. Mich. Mus. Pal., Contrib., 7(5): 91–105, 2 figs.

—— 1950. Mammals of the Rexroad Formation from Fox Canyon, Meade County, Kansas. *Ibid.*, 8(6): 113–192, 5 pls., 23 figs.

—— 1952. The Saw Rock Canyon Fauna and its Stratigraphic Significance. PMASAL, 38(1952): 387–411, 5 figs.

—— 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. *Ibid.*, 41 (1955): 145–200, 2 pls., 16 figs.

—— 1958. New Stratigraphic Names for Early Pleistocene Deposits in Southwestern Kansas. Am. Jour. Sci., 256: 54–59.

—— 1960. An Interpretation of Pliocene and Pleistocene Climates in North America. 62nd Ann. Report, Mich. Acad. Sci., Arts, and Let.: 5–30, 1 pl., 2 figs.

—— and Elmer S. Riggs. 1949. Upper Pliocene Vertebrates from Keefe Canyon, Meade County, Kansas. Geol. Soc. Am., Bull., 60: 829–860, 5 pls., 11 figs.

Osborn, Henry F. 1936. Proboscidea. Vol. 1. American Museum Press. 1–802, 12 pls., front., 680 figs.

Savage, Donald E. 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Panhandle of Texas, Part II: *Proboscidea*. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 31(3): 51–74, 2 pls., 8 figs.

Shotwell, J. Arnold. 1955. Review of the Pliocene Beaver *Dipoides*. Jour. Paleont., 29(1): 129–144, 6 figs.

Simpson, George G., and Carlos de Paula Couto. 1957. The Mastodonts of Brazil. Am. Mus. Nat. Hist., Bull., 112(2): 125–190, 23 pls., 11 figs., 13 tab.

Smith, H. T. U. 1940. Geological Studies in Southwestern Kansas. Kans. Geol. Surv., Bull., 34: 1–212, 34 pls., 22 figs.

Stirton, R. A. 1935. A Review of the Tertiary Beavers. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 23(13): 391–458, 142 figs., 1 map, 2 charts.

Taylor, Dwight W. 1960. Late Cenozoic Molluscan Faunas from the High Plains. U. S. Geol. Surv. Prof. Pap., 337: 1–94, 4 pls., 2 figs., 19 tab.

Wetmore, Alexander. 1944. Remains of Birds from the Rexroad Fauna of the Upper Pliocene of Kansas. Univ. Kans., Sci. Bull., 30(Pt. 1, No. 9): 89–105, 19 figs.

Plate I

Fig. 1. Contact (arrows) between Rexroad and Ballard formations in the SE¼, SW¼ Sec. 22, T. 33 S., R. 29 W., Meade County, Kansas. Consolidated Angell sands in contact with Rexroad on right, Missler silts in contact with Rexroad on left.

Fig. 2. Contact (arrows) between Rexroad formation and Missler silt of Ballard formation in NE¼, SE¼ Sec. 32, T. 33 S., R. 29 W., Meade County, Kansas.

PLATE I

FIG. 1

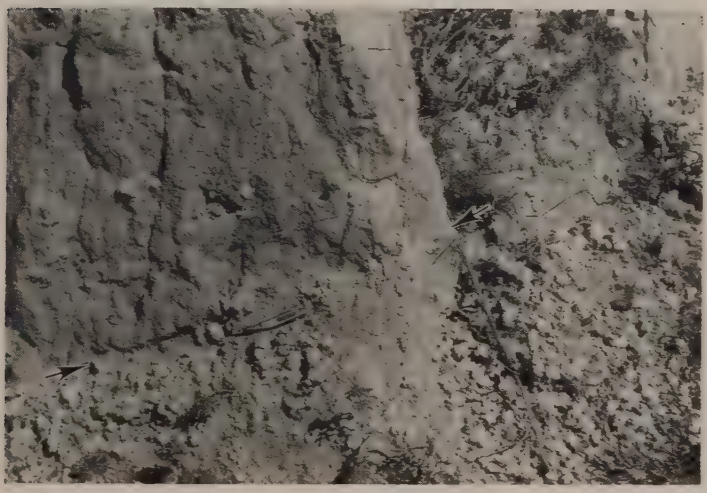

FIG. 2

PLATE II

Stegomastodon rexroadensis, sp. nov., UMMP 41207, holotype
FIG. 1. RM^2 and RM^3. $\times$-½.
FIG. 2. LM^2 and LM^3. $\times$-½.

PLATE III

Stegomastodon rexroadensis, sp. nov., UMMP 41207, holotype
FIG. 1. $LM_{\bar{2}}$ and $LM_{\bar{3}}$. $\times$-½.
FIG. 2. $RM_{\bar{2}}$ and $RM_{\bar{3}}$. $\times$-½.

PLATE IV

Stegomastodon rexroadensis, sp. nov.
FIG. 1. UMMP 29996, RM_2 . ×-½.
FIG. 2. KUMNH 4637, RM_1 and RM_2 . ×-½.

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A LATE PLEISTOCENE MOLLUSCAN FAUNULE FROM MEADE COUNTY, KANSAS

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A new molluscan faunule recovered from a Pleistocene deposit (locality UM-K4-53), situated in the SE ¼ Sec. 14, T. 32 S., R. 29 W., on the Big Springs Ranch, Meade County, Kansas, is here reported for the first time. The fossil-bearing material was removed by Claude W. Hibbard and members of the University of Michigan Museum of Paleontology field parties, during the summers of 1953 and 1957. Approximately one ton of matrix from this site was washed for the purpose of recovering the fossils, utilizing the techniques described in Hibbard (1949b). One half of the concentrate has been sorted and has yielded a large molluscan faunule composed of 30 genera and 53 species. Associated with the mollusks were ostracods; hackberry seeds (*Celtis*); and vertebrate remains of fishes (*Ictaluris* sp. and *Cyprinid* indet.), amphibians, mammals [*Sorex cinereus* Kerr, *Geomys* sp., *Peromyscus* cf. *P. berendsensis* Starrett, *Ondatra zibethicus* (Linnaeus), *Microtus pennsylvanicus* (Ord), *Pedomys ochrogaster* (Wagner), and *Synaptomys* (*Synaptomys*) sp.], as well as numerous unidentified pieces of bone. In June 1959, the locality was revisited and an additional three tons of matrix were removed and washed. Only the vertebrate fossils have been sorted from this concentrate.

The present study has had two immediate objectives: (1) the interpretation of the local habitat and climatic conditions in which the fossils lived, from inferences based on the geographic distribution and ecologic requirements of the extant elements of the molluscan faunule; (2) the comparison of the present faunule with four other late Pleistocene molluscan faunas, to determine if there are any quantitative differences distinguishing these assemblages that might be of use in stratigraphic correlation.

Stratigraphy

Description of sediments.—The sediments that have yielded the UM-K4-53 faunule are fine-grained sands, silts, and clays. The outcrop is exposed along the north bank of Spring Creek, about 2 miles

upstream from Mount Scott ("The Lookout"). There is no evidence that these deposits occur along the south bank of the creek. Followed downstream from the most westward exposure on the north side of Spring Creek, it consists of several linear outcrops, not exceeding 17 feet in thickness, with its base buried below the level of the present stream floor. The first of these exposures is 72 feet in length and consists of gray clays and sands; followed by a 345-foot covered interval composed of buff silts and clays; and finally by a 735-foot linear exposure of fine-grained, gray silts and clays.

The mollusks were recovered from a light-gray, silty clay zone, approximately 18 inches thick, which occurs in the 735-foot exposure. The fossil zone is situated from 2 to 3 feet above the bed of the stream. Weathered dry surfaces of the sediments from this bed are a buff-gray color and contain an orange limonitic stain. Fresh, moist surfaces are brown-gray in color.

The sediments containing the mollusks are believed to be part of a fluvial deposit laid down by a late Pleistocene stream that had become entrenched in the Crooked Creek formation (Kansan and Yarmouth age). The stream had downcut at least to the Angell member (Nebraskan) of the Ballard formation.

The deposit is interpreted as fluvial in origin for the following reasons: (1) The intermittent nature of the outcrop is suggestive of a meandering stream that followed a course similar to that of the present Spring Creek. (2) Downstream, near the base of Mount Scott, Hibbard and Taylor (1960) report that "undescribed fossils of glacial age occur in the base of the Kingsdown formation, stratigraphically below the Cragin Quarry local fauna with no evidence of an intervening gap in sedimentation." The mollusks recovered from this area were taken from a zone that is similar lithologically to the sediments which contained the faunule at the UM-K4-53 locality. At both localities, *Peromyscus* cf. *P. berendsensis* and *Synaptomys* (*Synaptomys*) sp. were found associated with the mollusks, suggesting that the deposits are equivalent in age. These similarities indicate that the two exposures were once possibly part of a single deposit of long linear extent that was laid down by the same stream. (3) The ecologic inferences based on the molluscan faunule fit very well with a fluvial origin for the deposit.

Age and correlation.—On the Big Springs Ranch, within an area of 6 square miles, a sequence of deposits ranging in age from late

Pliocene to late Pleistocene are exposed. The younger Pleistocene deposits occur as isolated valley fills and terrace deposits on the more extensive Crooked Creek and Ballard formations. The problem of dating and correlating these beds is considerable. Faunal criteria have not been adequately worked out for the Illinoian, Sangamon, and Wisconsin, to permit differentiation of beds by this means, and correlating outcrops by "walking them out" is usually not feasible in this area, where the beds are not traceable for more than a short distance. These difficulties have been encountered in the efforts made to date the mollusks, thus making assignment of the faunule to a specific age tentative.

Environmental inferences based on a study of the mollusks and the associated vertebrates indicate that the faunule represents cooler, moister conditions than now exist in the area. Many of the animals are now found living to the north and/or east of Meade County, giving the assemblage a definite glacial aspect.

The deposit in which the mollusks occur is post-Crooked Creek in age and is probably part of the Kingsdown formation (Hibbard, 1949a), on the basis of stratigraphic and paleontologic evidence. The contact between the overlying buff silts and clays and the underlying gray sands, silts, and clays is very irregular. Although the sediments overlying the fossil deposit have not been studied in detail and no fossils have been found in these upper beds to permit dating by this means, the irregular nature of the contact suggests that another cycle of erosion and deposition took place sometime after the deposition of the gray sands, silts, and clays. If this interpretation is correct, then the first cycle should have taken place during the Illinoian and Sangamon and the second during Wisconsin time. The caliche layer associated with the Sangamon in the Butler Spring and Cragin Quarry localities (Hibbard and Taylor, 1960) is not present at the UM-K4-53 locality, suggesting that the upper part of the Kingsdown formation representing Sangamon time was removed during a later erosional cycle, before the upper buff silts were deposited.

Recent work during the 1959 field season has recovered remains of *Peromyscus* cf. *P. berendsensis*, from both the base of Mount Scott and the UM-K4-53 locality. *P. berendsensis* has previously been known only from the Berends local fauna (Starrett, 1956), of Illinoian age. Its presence at these two new localities is considered strong evidence of an Illinoian age.

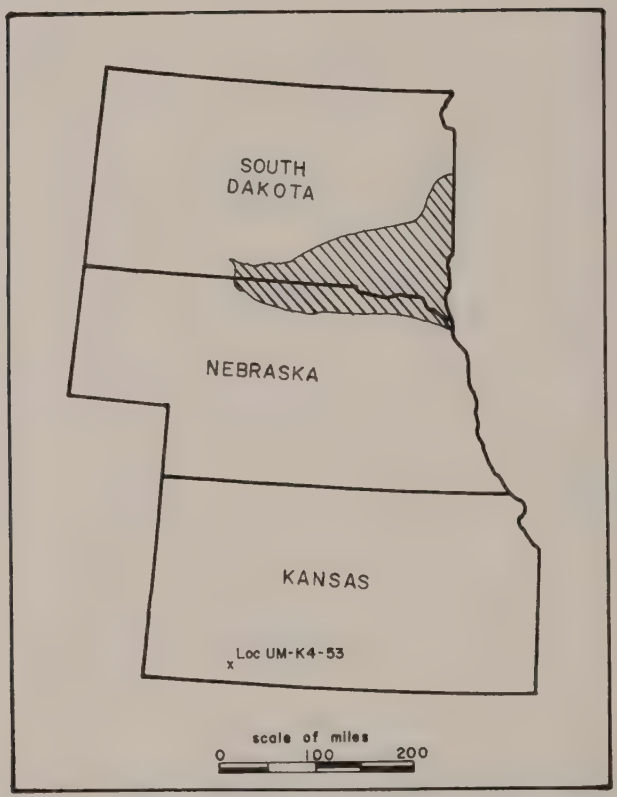

FIG. 1. A map showing the estimated amount of faunal shift between the overlap area, represented by the shading, and the UM-K4-53 locality.

MOLLUSKS FROM LOCALITY UM-K4-53

Space limitations prohibit detailed presentation of data on geologic range, geographic distribution, ecologic requirements, and systematics of each species. This information is available in Pilsbry (1946, 1948), F. C. Baker (1928a), Leonard (1959), Hibbard and Taylor (1960), and Taylor (1960) for the gastropods; Herrington and Taylor (1958) and Herrington (in press) for the sphaeriids; and F. C. Baker (1928b) and Simpson (1914) for the unionids.

The paleoecologic interpretations made on the UM-K4-53 mollusks are based on the distributional and ecologic data obtained from these sources for the extant elements of the faunule.

Following is a list of species and catalogue numbers for the UM-K4-53 mollusks. The specimens are housed in the University of Michigan Museum of Zoology (UMMZ).

CLASS PELECYPODA

Order Prionodesmacea
Uniomerus cf. *tetralasmus* (Say)—UMMZ 200649
Order Teleodesmacea
Sphaerium lacustre (Müller)—UMMZ 200642
S. occidentale Prime—UMMZ 200643
S. rhomboideum (Say)—UMMZ 200644
S. striatinum (Lamarck)—UMMZ 200645
S. sulcatum (Lamarck)—UMMZ 200646
Pisidium casertanum (Poli)—UMMZ 200628
P. compressum Prime—UMMZ 200629
P. nitidum Jenyns—UMMZ 200630a, 200630b
P. obtusale Pfeiffer—UMMZ 200631
P. subtruncatum Malm—UMMZ 200632
P. variabile Prime—UMMZ 200633
P. walkeri Sterki—UMMZ 200634

CLASS GASTROPODA

Order Mesogastropoda
Valvata tricarinata (Say)—UMMZ 200652
Order Basommatophora
Carychium exiguum (Say)—UMMZ 200603
Stagnicola caperata (Say)—UMMZ 200647
S. cf. *reflexa* (Say)—UMMZ 200648
Fossaria dalli (Baker)—UMMZ 200608
F. obrussa (Say)—UMMZ 200609
Gyraulus circumstriatus (Tryon)—UMMZ 200616, 200617a
G. parvus (Say)—UMMZ 200618, 200617b
Armiger crista (Linne)—UMMZ 200602
Helisoma anceps (Menke)—UMMZ 200621
H. trivolvis (Say)—UMMZ 200622
**Promenetus* cf. *kansasensis* (Baker)—UMMZ 200635
Physa anatina Lea—UMMZ 200625
P. gyrina Say—UMMZ 200626
P. skinneri Taylor—UMMZ 200627
Aplexa hypnorum (Linne)—UMMZ 200601

* Species extinct.

Ferrissia meekiana (Stimpson)—UMMZ 200607
Laevapex fuscus (Adams)—UMMZ 200623
Order Stylommatophora
Strobilops labyrinthica (Say)—UMMZ 200640
Gastrocopta armifera (Say)—UMMZ 200610
G. contracta (Say)—UMMZ 200611
G. cristata (Pilsbry and Vanatta)—UMMZ 200612
G. holzingeri (Sterki)—UMMZ 200613
G. procera (Gould)—UMMZ 200614
G. tappaniana (Adams)—UMMZ 200615
Pupoides albilabris (Adams)—UMMZ 200637
Pupilla blandi Morse—UMMZ 200638
Vertigo milium (Gould)—UMMZ 200653
V. ovata Say—UMMZ 200654
Vallonia gracilicosta Reinhardt—UMMZ 200650
V. parvula Sterki—UMMZ 200651
cf. *Succinea*—UMMZ 200641
Oxyloma retusa (Lea)—UMMZ 200624
Discus cronkhitei (Newcomb)—UMMZ 200605
Helicodiscus parallelus (Say)—UMMZ 200620
Punctum minutissimum (Lea)—UMMZ 200636
* *Deroceras aenigma* Leonard—UMMZ 200604
Euconulus fulvus (Müller)—UMMZ 200606
Retinella electrina (Gould)—UMMZ 200639
Hawaiia minuscula (Binney)—UMMZ 200619
Zonitoides arboreus (Say)—UMMZ 200655

Analysis of fauna.—The UM-K4-53 molluscan faunule is composed of 53 species, of which 13 are pelecypods; 18 are freshwater, and 22, terrestrial gastropods. Two of the species, *Promenetus kansasensis* and *Deroceras aenigma*, are now extinct; 3 species, *Uniomerus tetralasmus*, *Sphaerium rhomboideum*, and *Pisidium variabile*, represent new fossil occurrences for the High Plains; and the range of 2 species, *Pisidium subtruncatum* and *Punctum minutissimum*, are recorded for the first time from the Illinoian. Only 17 of the 53 species of the faunule are still living in the Meade County area (Hibbard and Taylor, 1960).

Approximately 61 per cent of the total number of individuals present are aquatic forms. Three aquatic species, *Valvata tricarinata* (10.13 per cent), *Gyraulus circumstriatus* (13.22 per cent), and *G. parvus* (19.69 per cent), constitute 43.04 per cent of the mollusks in the faunule.

A comparison of the faunule from locality UM-K4-53, with four

TABLE I

FIVE LATE PLEISTOCENE MOLLUSCAN FAUNAS FROM MEADE COUNTY, KANSAS

The numbers represent individual specimens for each species. Numbers in excess of 200 have been estimated volumetrically for the UM-K4-53 faunule. Integers are used to indicate specimens of pelecypods that have both valves intact. Fractions indicate the number of separate pelecypod valves.

Species	Butler Spring l.f.			Cragin Quarry l.f.				Jingle-bob	Jones	UM-K4-53
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4	l.f.	l.f.	faunule
Valvata tricarinata (Say)	74,085	17	—	—	—	—	—	1	58	3,600
Probythinella lacustris (Baker)	2	—	—	—	—	—	—	—	—	-
Carychium exiguum (Say)	81	—	—	4,500	3,200	4	—	300	—	1,500
Lymnaea stagnalis jugularis Say	1	—	—	—	—	—	—	—	?	—
Stagnicola caperata (Say)	300	2	—	500	95	18	2	100	21	1,200
S. cockerelli (Pilsbry and Ferriss)	—	—	—	—	—	—	—	—	7	—
S. exilis (Lea)	—	—	—	600	—	—	—	—	—	—
S. palustris (Müller)	—	—	—	—	—	—	—	cf. 2	17	—
S. reflexa (Say)	243	—	—	—	—	—	—	—	—	cf. 12
Fossaria dalli (Baker)	21	3	—	104	18	—	—	60	6	159
F. obrussa (Say)	140	—	—	—	—	—	—	41	—	90
Anisus pattersoni (Baker)	36	—	—	—	—	—	—	—	—	—
Armiger crista (Linne)	—	—	—	—	—	1	—	—	9	19
Gyraulus circumstriatus (Tryon)	600	—	—	2,000	55	37	1	500	5	4,700
G. parvus (Say)	49,500	24	—	—	—	—	—	100	300	7,000
Helisoma anceps (Menke)	2	—	—	—	—	—	—	50	—	161
H. trivolvis (Say)	46	—	—	26	—	—	—	33	20	10
Promenetus exacuous (Say)	—	—	—	—	—	—	—	50	11	—
P. kansasensis (Baker)	1,200	3	—	3,200	—	5	—	—	—	cf. 500
P. umbilicatellus (Cockerell)	57	—	—	2,000	—	—	—	—	1	—
Physa anatina Lea	7,500	85	—	136	14	1	—	cf. 50	375	320
P. gyrina Say	325	—	—	47	—	—	—	100	11	270
P. skinneri Taylor	19	—	—	—	—	—	—	—	—	3
Apleza hypnorum (Linne)	3	—	—	—	—	—	—	15	?	142
Ferrissia meekiana (Stimpson)	6	—	—	17	—	—	—	3	—	4
F. rivularis (Say)	—	—	—	—	—	—	—	2	—	—
Laevapex fuscus (Adams	—	—	—	—	—	—	—	6	1	17
L. kirklandi (Walker)	221	—	—	—	—	—	—	2	—	—
Strobilops labyrinthica (Say)	—	—	—	—	—	—	—	150	—	338
Gastrocopta armifera (Say)	200	—	—	6	400	42	23	200	21	1,500
G. contracta (Say)	19	—	—	226	250	3	1	100	—	830
G. cristata (Pilsbry & Vanatta)	800	1	—	89	1,000	1,000	4	300	2	980
G. holzingeri (Sterki)	49	—	—	92	1,000	73	—	50	—	710
G. pellucida hordeacella (Pilsbry)	—	—	—	4	9	600	—	—	—	—
G. procera (Gould)	23	1	—	—	—	—	—	5	?	230
G. tappaniana (Adams)	300	19	—	2,800	2,000	49	4	300	—	2,100
Pupoides albilabris (Adams)	200	—	—	8	3	162	2	100	100	620
P. inornatus (Vanatta)	44	—	—	—	—	—	—	—	3	—
Pupilla blandi Morse	27	9	—	—	—	9	—	2	86	1
P. muscorum (Linne)	78	4	—	—	—	—	—	—	—	—
P. sinistra Franzen	1	4	—	—	—	—	—	—	—	—
Vertigo gouldi (Binney)	1	—	—	—	—	—	—	—	—	—
V. milium (Gould)	45	73	—	2	1	2	—	100	—	245
V. ovata (Say)	300	4	—	500	48	3	3	150	5	1,280

TABLE I—*Continued*

Species	Butler Spring l.f.			Cragin Quarry l.f.				Jinglebob	Jones	UM-K4-53
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4	l.f.	l.f.	faunule
Vallonia cyclophorella (Sterki)	375	27	—	—	—	—	—	—	—	—
V. gracilicosta Reinhardt	175	12	—	7	—	600	—	150	250	800
V. parvula Sterki	200	—	—	1,200	1,500	180	3	50	—	561
cf. *Succinea*	1,200	26	—	300	145	13	4	120	300	66
Ozyloma retusa (Lea)	17	—	—	—	—	—	—	6	—	143
Discus cronkhitei (Newcomb)	4	2	—	—	—	—	—	—	—	2
Helicodiscus parallelus (Say)	—	—	—	7	6	600	2	50	—	280
H. singleyanus (Pilsbry)	72	3	—	1	—	900	1	—	—	—
Punctum minutissimum (Lea)	—	—	—	—	—	—	—	35	—	43
Deroceras aenigma Leonard	—	—	—	3,200	38	6	1	2	—	200
D. laeve (Müller)	—	—	—	—	—	—	—	28	—	—
Euconulus fulvus (Müller)	—	—	—	182	46	1	—	20	—	84
Retinella electrina (Gould)	—	—	—	40	12	2	—	16	—	107
Hawaiia minuscula (Binney)	400	17	—	4,800	2,000	400	25	200	150	2,300
Zonitoides arboreus (Say)	51	—	—	40	14	1	1	40	—	250
Stenotrema leai (Binney)	68	—	—	575	222	1	29	1	—	—
Sphaerium lacustre (Müller)	—	—	—	—	—	—	—	—	—	12/2
S. occidentale Prime	—	—	—	—	—	—	—	12/2	—	1/2
S. partumeium (Say)	—	—	—	63/2	—	—	—	3/2	—	—
S. rhomboideum (Say)	—	—	—	—	—	—	—	—	—	1/2
S. striatinum (Lamarck)	50/2	—	—	—	—	—	—	1/2	—	14/2
S. sulcatum (Lamarck)	—	—	—	—	—	—	—	29/2	—	54/2
S. transversum (Say)	5/2	—	—	—	—	—	—	—	—	—
Pisidium casertanum (Poli)	29/2	—	—	1200/2	—	7/2	1/2	2658/2	—	600/2
P. compressum Prime	1 + 731/2	—	—	—	—	—	—	109/2	30/2	1095/2
P. ferrugineum Prime	—	—	—	—	—	—	—	—	1/2	—
P. lilljeborgi Clessin	—	—	—	—	—	—	—	—	6/2	—
P. nitidum Jenyns	221/2	—	—	—	—	—	—	20/2	2/2	325/2
P. obtusale Pfeiffer	—	—	—	—	—	—	—	29/2	—	63/2
P. subtruncatum Malm	—	—	—	—	—	—	—	—	—	1/2
P. variabile Prime	—	—	—	—	—	—	—	—	—	9/2
P. walkeri Sterki	1/2	—	—	—	—	—	—	8/2	261/2	1/2
Anodonta grandis Say ?	2/2	—	—	—	—	—	—	2/2	—	—
Uniomerus tetralasmus (Say)	—	—	—	—	—	—	—	—	—	cf. 2/2
Quadrula quadrula (Rafinesque)	—	—	1/2	—	—	—	—	—	—	—

other late Pleistocene molluscan faunas (Tab. I), on the sole basis of species represented, revealed that it has 38 species in common with the Butler Spring local fauna; 28 with the Cragin Quarry local fauna; 44 with the Jinglebob local fauna; and 21 with the Jones local fauna (Tab. VI).

The presence of *Valvata tricarinata, Stagnicola caperata, Gyraulus circumstriatus, Armiger crista, Aplexa hypnorum, Discus cronkhitei, Retinella electrina, Vallonia gracilicosta, Punctum minu-*

tissimum, Sphaerium occidentale, S. rhomboideum, Pisidium subtruncatum, and *P. walkeri*, which are all presently distributed well to the north of Meade County, suggests that moist, cool, glacial conditions prevailed. The presence of shells referable to *Promenetus kansasensis*, which is unknown, so far, from deposits younger than the Sangamon in the High Plains area, indicates a probable Illinoian age for the faunule.

Paleoecology

Local environment.—The mollusks have been divided into groups which are considered to represent nine relatively distinct habitats (Tab. II). This division is artificial, since very few of the species are always restricted to the one habitat to which they are assigned here, but the assumption that each mollusk species does have a certain "preferred" habitat in which it most commonly occurs, and to which it may be assigned, is believed to be essentially a valid one.

The occurrence of *Valvata tricarinata, Sphaerium lacustre, S. striatinum, Pisidium compressum, P. subtruncatum, P. variabile*, and *Helisoma anceps*, all species that require a permanent water situation, is interpreted as indicating the presence, sometime during Illinoian time, of a perennial stream approximately the same size as the present Spring Creek. The stream in this area had a depth of perhaps 1 to 3 feet, with a slow to moderate current, and a substrate of soft sand and mud. The existence of shallow spots, with little or no current action, or of areas with dense rooted vegetation that considerably reduced the effects of the current are indicated by the presence of *Gyraulus parvus, Sphaerium rhomboideum, S. sulcatum, Pisidium obtusale, Physa anatina, P. skinneri*, and *Laevapex fuscus*.

Many of the *Pisidium casertanum* are marked with prominent "rest marks," which are generally considered indicative of a fluctuating water level. This, with the presence of *Sphaerium occidentale, Stagnicola caperata, S. reflexa, Gyraulus circumstriatus, Physa gyrina, Aplexa hypnorum, Armiger crista*, and *Ferrissia meekiana*, species that are usually associated with temporary water situations, suggests that a slough or temporary pond must have been present somewhere near the stream, perhaps on the adjacent flood plain.

Zonitoides arboreus, Retinella electrina, Euconulus fulvus, Strobilops labyrinthica, Punctum minutissimum, and *Helicodiscus parallelus*, all terrestrial snails that typically inhabit woodland situations,

TABLE II

SUMMARY OF LOCAL HABITATS REPRESENTED BY THE MOLLUSKS OF THE UM-K4-53 FAUNULE

The numbers indicate the per cent of each species in the faunule (modified from Taylor, in Hibbard and Taylor, 1960)

Habitat	Species	Per Cent
Semiaquatic: among vegetation and debris near water's edge.	*Oxyloma retusa*	0.40
Hygrophilic: moist situations in leaf mold, under sticks and debris; shaded areas; not far from water.	*Carychium exiguum*	4.22
	Vertigo ovata	3.60
	V. milium	0.69
	Gastrocopta tappaniana	5.91
	Deroceras aenigma	0.56
Woodland habitat: moist areas under leaf litter, down timber, or in marsh grass.	*Discus cronkhitei*	-
	Zonitoides arboreus	0.70
	Retinella electrina	0.30
	Euconulus fulvus	0.24
	Strobilops labyrinthica	0.95
	Punctum minutissimum	0.12
	Helicodiscus parallelus	0.79
Sheltered areas: live among rocks, shrubs, grass, or in timbered situations.	*Gastrocopta armifera*	4.22
	G. procera	0.65
	G. contracta	2.33
	G. holzingeri	1.10
Sheltered situations: these species are not restricted to a woodland habitat and can tolerate drier conditions.	*G. cristata*	2.76
	Pupoides albilabris	1.74
	Hawaiia minuscula	6.47
	Pupilla blandi	-
	Vallonia parvula	1.58
	V. gracilicosta	2.25
Marginal situations: wet mud; sticks, stones, or any other debris along water's edge; shallow pools and protected spots.	*Fossaria dalli*	0.45
	F. obrussa	0.25
Shallow, quiet water: small streams, ponds, or sloughs that may become dry during part of the year.	*Pisidium casertanum*	1.69
	Sphaerium occidentale	-
	Stagnicola caperata	3.38
	Gyraulus circumstriatus	13.22
	Physa gyrina	0.76
	Apleza hypnorum	0.40
	Armiger crista	0.05
	Ferrissia meekiana	0.01

TABLE II—*Continued*

Habitat	Species	Per Cent
Shallow, quiet water: small ponds, streams, or sloughs with no current or areas of rooted vegetation with little current; soft-sand or mud bottoms; not subject to significant seasonal drying.	*Uniomerus tetralasmus*	—
	Sphaerium rhomboideum	—
	S. sulcatum	0.15
	Pisidium obtusale	0.18
	Gyraulus parvus	19.69
	Helisoma trivolvis	0.03
	Promenetus kansasensis	1.41
	Physa anatina	0.90
	P. skinneri	0.01
	Laevapex fuscus	0.05
Perennial stream: slow to moderate current; areas of still water; shallow spots with soft sand or mud substrate; not affected by seasonal drying.	*Sphaerium lacustre*	0.03
	S. striatinum	0.04
	Pisidium compressum	3.08
	P. nitidum	0.91
	P. subtruncatum	—
	P. variabile	0.03
	P. walkeri	—
	Valvata tricarinata	10.13
	Helisoma anceps	0.45

constitute 3.10 per cent of the total number of individuals in the faunule. The relatively unworn condition of the shells of these species suggests that they have been transported but a short distance and that somewhere near the stream there must have existed a woods. This woodland need not have been very extensive and may have merely bordered the stream.

Climate.—The climatic conditions under which the mollusks lived may, to some degree, be inferred from the distributional pattern of the extant elements of the faunule and the characteristics of the local environment.

The climatic interpretation derived from the distribution patterns of Recent mollusks is based primarily on the following two assumptions: (1) that it is possible to recognize the effects of climatic factors as the agents controlling the geographic ranges of some of the living species of mollusks; and (2) that the area in the Interior Plains nearest the fossil locality, where the largest number of species contained in the fossil faunule are presently living, will most closely

simulate the climatic conditions that existed at the time the UM-K4-53 mollusks lived.

Many of the species, because of their wide distribution or because they are now living in the Meade County area (see molluscan faunal list for Meade County in Hibbard and Taylor, 1960), are believed to be of little value as indicators of climatic change. With the exception of *Gastrocopta cristata* and *G. procera*, which because of their southern distribution pattern are considered climatically significant, none of the species in the faunule that are now living in the area is used. Of the remaining species, only those with restricted ranges are considered.

The UM-K4-53 faunule is composed of several groups of mollusks with different distributional patterns. When considered in terms of individual numbers and climatic significance, two components seem to dominate the faunule. These are: (1) a northern element, composed of 13 species, the north-south distribution of which is believed to be controlled primarily by temperature extremes; and (2) an eastern group, containing 5 species, in which the east-west distribution appears to be related to humidity.

Included in the northern segment are *Valvata tricarinata*, *Gyraulus circumstriatus*, *Armiger crista*, *Stagnicola caperata*, *Aplexa hypnorum*, *Discus cronkhitei*, *Retinella electrina*, *Punctum minutissimum*, *Vallonia gracilicosta*, *Sphaerium occidentale*, *S. rhomboideum*, *Pisidium subtruncatum*, and *P. walkeri*. These species are presently known to extend at least as far south as north-central Nebraska, to about 42° north latitude in the central Interior Plains. The molluscan fauna of Nebraska is so poorly known that it is quite possible that future collecting in this area will extend the range of some species farther to the south. None of these species, however, has been reported from northwestern Kansas, where the molluscan fauna is relatively well known (Leonard, 1959).

Five of these species, *Gyraulus circumstriatus*, *Discus cronkhitei*, *Retinella electrina*, *Punctum minutissimum*, and *Vallonia gracilicosta*, have been able to maintain their ranges southward in the Rocky Mountains. Their north-south distribution in the southern Interior Plains, therefore, appears to be controlled by the high summer temperatures that characterize this region.

The failure of the other northern species to become similarly established in the mountains may be due to a scarcity of suitable

aquatic habitats. This explanation, however, does not seem applicable to *Armiger crista, Stagnicola caperata, Aplexa hypnorum,* and *Sphaerium occidentale,* for over other parts of their range they are often found in association with *Gyraulus circumstriatus.* The distribution of these species is perhaps controlled by some complex interaction of factors involving nutrients and climate.

A second group of species, composed of *Carychium exiguum, Gastrocopta contracta, Vertigo milium, Ferrissia meekiana,* and *Laevapex fuscus,* constitutes an eastern element in the faunule.

The western extension of these species in the Interior Plains is apparently controlled by humidity. The absence of these species from the Recent molluscan fauna of Meade County, and their ability to extend far to the south of the latitude represented by the fossil locality, along the more humid East Coast and Mississippi River Valley, is considered indicative of a significant decrease in the amount of effective moisture available to the mollusks since the time the faunule lived.

A postulated local environment, in which a perennial stream, temporary water situations, and some wooded areas were present, is required to account for the composition of the UM-K4-53 faunule. The presence of these habitats suggests that the area during Illinoian time was characterized by moister, cooler summers than presently exist.

The central and eastern part of the Nebraska-South Dakota border (Fig. 1), is the general region in which southern (represented by *Gastrocopta cristata* and *G. procera*) and northern elements (see above) reach the northern and southern limits of their respective ranges. Most of the species present in the faunule (41 species) are now found within the area of overlap, although not necessarily at any one specific locality (Over, 1915; Roscoe, 1954, 1955; Jones, 1932; Hibbard and Taylor, 1960; and Taylor, 1960).

The discrepancy between the number of species present in the faunule and the overlap area is possibly due to several factors: (1) two of the species, *Deroceras aenigma* and *Promenetus kansasensis,* are now extinct; (2) human activities in the area (cultivation, drainage, and overgrazing of the land, etc.) may have caused a disruption of the natural biotic communities, which prevent similar assemblages of mollusks from existing today; (3) some of the species may be still living in the region but because of inadequate collecting from this

area have not been reported; and (4) physiological evolutionary changes in some species may have produced certain alterations in their environmental tolerances, which have resulted in different faunal associations. It seems quite reasonable to assume in the absence of any conflicting data that the climatic conditions represented by the mollusks were similar to those now prevailing in the area of overlap.

Analyses of the temperature, evapotranspiration, and precipitation rates in the overlap area and Meade County suggest that the most significant differences between the two regions are the result of the relative temperature and moisture extremes that occur during the summer months. (These climatic differences are summarized in Table III.)

The normal summer temperature in the area of overlap is 5° cooler than in Meade County. This region receives between 20 and 30 inches of precipitation per year, the largest part of which falls during the summer months when it is most needed. Added to the ameliorating effects of a higher summer precipitation rate is the lower evaporation rate from surface water (reservoirs, shallow lakes, etc.), which further increases the effectiveness of the precipitation. These factors all combine to produce cooler, more humid summer conditions in the overlap area.

The composition of the UM-K4-53 molluscan faunule reflects the existence during Illinoian time of similar climatic conditions several hundred miles to the south in the Meade County area. The cooler, moister summers permitted species that are predominantly northern or eastern or both in their distribution to range into the southern High Plains region.

The postulated summer climatic conditions were similar to those now existing in the overlap area, with a normal temperature of between 70° and 75° F., and about 20 to 30 inches of precipitation annually, 40 to 50 per cent of which fell during the summer months. The normal winter temperature during this part of the Illinoian was probably no colder than that now occurring in the area of overlap (between 15° and 25° F.). This interpretation is based on the presence of *Gastrocopta cristata* and *G. procera*, which represent a relatively southern element in the faunule. The absence of these two species from assemblages to the north of the overlap area is believed to be controlled by the cold winters. If winters during the Illinoian were

TABLE III

Summary of Climatic Differences Between the Meade County and Overlap Areas*

	Meade County Area	Overlap Area
Temperature		
Annual temperature	55°–60°	45°–50°
Normal winter temperature	25°–35°	15°–25°
Normal summer temperature	75°–80°	70°–75°
Normal annual number of days with maximum temperatures of 90° or higher	70 days	25 days
Normal annual number of days with daily maximum temperatures above 85°	90 days	62 days
Evaporation		
July average minimum relative humidity	30%–40%	40%–50%
Normal annual evaporation from reservoirs and shallow lakes	50″–70″	40″–50″
Normal July evaporation from reservoirs and shallow lakes	10″–12″	6″–8″
Normal annual excess of precipitation over evaporation	less than 0″	0″–10″
Normal evaporation during warm season, April to September	50″–60″	35″–40″
Mean difference between precipitation and evaporation from April to October	−40″ to −50″	−10″ to −30″
Precipitation		
Normal annual precipitation	20″–30″	20″–30″
Per cent of precipitation that occurs in summer	30%–40%	40%–50%
Normal summer precipitation	6″–8″	8″–12″

* Based on climatic maps in Visher, 1954.

much cooler than they are at present, it would be difficult to explain how these species could have ranged far enough to the north to occur in an otherwise predominantly northern assemblage.

Comparison of Five Late Pleistocene Molluscan Faunas

An age determination, based on the quantitative relationships of the UM-K4-53 molluscan faunule, to the Butler Spring local fauna (Illinoian), the Cragin Quarry local fauna (Sangamon), the Jinglebob local fauna (Sangamon), and the Jones local fauna (Wisconsin)

has been attempted. The five faunas were analyzed and compared for: (1) the percentage of species shared in common; (2) the percentage of total specimens represented by each species; and (3) the percentage of terrestrial to aquatic species, to see if any significant patterns would develop that might provide a means of correlating faunas of the same age. The results are summarized in Tables I, IV, V, and VI.

Method of study.—Both the faunal list and the number of specimens presented in Table I form the basic material for the study. This table represents a compilation of data from the following sources: the Butler Spring local fauna and the Cragin Quarry local fauna, Hibbard and Taylor (1960); the Jinglebob local fauna, van der Schalie (1953), Herrington and Taylor (1958), Hibbard and Taylor (1960), and the collection of the University of Michigan Museum of Zoology; the Jones local fauna, Goodrich (1940), Herrington and Taylor (1958), Hibbard and Taylor (1960), and specimens in the University of Michigan Museum of Zoology. The UM-K4-53 faunule is based on data compiled in connection with the materials studied.

Analysis.—A comparison of the proportion of individuals of each species in a fauna (Tab. IV), a relationship that should be more significant than a simple comparison of species present, failed to reveal any positive pattern that might be useful in correlating faunas.

The relationship between terrestrial and aquatic species (Tab. V) is not distinctive enough to permit correlation by this means. The proportion of terrestrial to aquatic species is evidently more a function of local habitat than age.

Analysis of Table VI reveals that correlations based on the percentage of species shared in common are not reliable. While the Butler Spring local fauna does appear to be most closely related to the UM-K4-53 mollusks, as does the Cragin Quarry to the Jinglebob, the UM-K4-53 faunule shares the greatest percentage of species in common with the Jinglebob.

This apparent lack of any distinguishing characteristics in the composition of the faunas may be due to several factors: (1) Differences in the amount of matrix recovered, washed, and sorted from each locality may have introduced an error in sampling. The larger the sample, the greater are the chances of recovering the less common species and of thereby increasing the faunal list. (2) Some of the dissimilarities between faunas are the result of comparing assem-

TABLE IV

A Comparison of the Per Cent of Total Individuals of Each Species for Five Late Pleistocene Molluscan Faunas

The (X) indicates that the species contained less than .01 per cent of the total number of individuals in the fauna

Species	Butler Spring l. f.			Cragin Quarry l. f.				Jingle-bob	Jones	UM-K4-53
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4	l. f.	l. f.	faunule
Valvata tricarinata (Say)	52.89	5.06	—	—	—	—	—	0.02	2.81	10.13
Probythinella lacustris (Baker)	X	—	—	—	—	—	—	—	—	—
Carychium exiguum (Say)	0.06	—	—	15.80	26.50	0.08	—	4.64	—	4.22
Lymnaea stagnalis jugularis Say	X	—	—	—	—	—	—	—	?	—
Stagnicola caperata (Say)	0.21	0.59	—	1.76	0.79	0.38	1.87	1.56	1.02	3.38
S. cockerelli (Pilsbry and Ferriss)	—	—	—	—	—	—	—	—	0.34	—
S. exilis (Lea)	—	—	—	2.11	—	—	—	—	—	—
S. palustris (Müller)	—	—	—	—	—	—	—	0.03	0.84	—
S. reflexa (Say)	0.17	—	—	—	—	—	—	—	—	0.03
Fossaria dalli (Baker)	0.02	0.89	—	0.37	0.16	—	—	0.93	0.29	0.45
F. obrussa (Say)	0.10	—	—	—	—	—	—	0.63	—	0.25
Anisus pattersoni (Baker)	0.03	—	—	—	—	—	—	—	—	—
Armiger crista (Linné)	—	—	—	—	—	0.02	—	—	0.44	0.05
Gyraulus circumstriatus (Tryon)	0.43	—	—	7.02	0.46	0.78	0.93	7.75	0.24	13.22
G. parvus (Say)	35.34	7.14	—	—	—	—	—	1.56	14.57	19.69
Helisoma anceps (Menke)	X	—	—	—	—	—	—	0.79	—	0.45
H. trivolvis (Say)	0.03	—	—	0.09	—	—	—	0.51	0.97	0.03
Promenetus exacuous (Say)	—	—	—	—	—	—	—	0.79	0.53	—
P. kansasensis (Baker)	0.86	0.89	—	11.24	—	0.11	—	—	—	1.41
P. umbilicatellus (Cockerell)	0.04	—	—	7.02	—	—	—	—	0.05	—
Physa anatina Lea	5.35	25.30	—	0.48	0.12	0.02	—	0.79	18.21	0.90
P. gyrina Say	0.23	—	—	0.17	—	—	—	1.56	0.53	0.76
P. skinneri Taylor	0.01	—	—	—	—	—	—	—	—	0.01
Aplexa hypnorum (Linne)	X	—	—	—	—	—	—	0.23	?	0.40

TABLE IV—*Continued*

Species	Butler Spring l. f.			Cragin Quarry l. f.				Jingle-bob	Jones	UM-K4-53
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4	l. f.	l. f.	faunule
Ferrissia meekiana (Stimpson)	X	—	—	0.06	—	—	—	0.05	—	0.01
F. rivularis (Say)	—	—	—	—	—	—	—	0.03	—	—
Laevapex fuscus (Adams)	—	—	—	—	—	—	—	0.09	0.05	0.05
L. kirklandi (Walker)	0.16	—	—	—	—	—	—	0.03	—	—
Strobilops labyrinthica (Say)	—	—	—	—	—	—	—	2.32	—	0.95
Gastrocopta armifera (Say)	0.14	—	—	0.12	3.31	0.89	21.50	3.10	1.02	4.22
G. contracta (Say)	0.01	—	—	0.79	2.07	0.06	0.93	1.55	—	2.33
G. cristata (Pils. and Van.)	0.57	0.30	—	0.31	8.28	21.19	3.73	4.64	0.10	2.76
G. holzingeri (Sterki)	0.03	—	—	0.32	8.28	1.55	—	0.77	—	1.10
G. pellucida hordeacella (Pils.)	—	—	—	0.01	0.07	12.71	—	—	—	—
G. procera (Gould)	0.02	0.30	—	—	—	—	—	0.81	?	0.65
G. tappaniana (Adams)	0.21	5.65	—	9.83	16.56	1.04	3.73	4.64	—	5.91
Pupoides albilabris (Adams)	0.14	—	—	0.03	0.02	3.43	1.87	1.55	4.86	1.74
P. inornatus (Vanatta)	0.03	—	—	—	—	—	—	—	0.05	—
Pupilla blandi Morse	0.02	2.67	—	—	—	0.19	—	0.03	4.18	X
P. muscorum (Linne)	0.06	1.19	—	—	—	—	—	—	—	—
P. sinistra Franzen	X	1.19	—	—	—	—	—	—	—	—
Vertigo gouldi (Binney)	X	—	—	—	—	—	—	—	—	—
V. milium (Gould)	0.03	21.72	—	X	X	0.04	—	1.55	—	0.69
V. ovata (Say)	0.21	1.19	—	1.76	0.40	0.06	2.80	2.32	0.24	3.60
Vallonia cyclophorella (Sterki)	0.27	8.04	—	—	—	—	—	—	—	—
V. gracilicosta Reinhardt	0.12	3.57	—	0.02	—	12.71	—	2.32	12.14	2.25
V. parvula Sterki	0.14	—	—	4.21	12.42	3.81	2.80	0.77	—	1.58
cf. *Succinea*	0.86	7.74	—	1.05	1.20	0.28	3.74	1.86	14.57	0.19
Oxyloma retusa (Lea)	0.01	—	—	—	—	—	—	0.09	—	0.40
Discus cronkhitei (Newcomb)	X	0.60	—	—	—	—	—	—	—	X
Helicodiscus parallelus (Say)	—	—	—	0.02	0.05	12.71	1.87	0.77	—	0.79

TABLE IV—*Continued*

Species	Butler Spring l. f.			Cragin Quarry l. f.				Jingle-bob	Jones	UM-K4-53
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4	l. f.	l. f.	faunule
H. singleyanus (Pilsbry)	0.05	0.89	—	X	—	19.07	0.93	—	—	—
Punctum minutissimum (Lea)	—	—	—	—	—	—	—	0.54	—	0.12
Deroceras aenigma Leonard	—	—	—	11.24	0.31	0.13	0.93	0.03	—	0.56
D. laeve (Müller)	—	—	—	—	—	—	—	0.43	—	—
Euconulus fulvus (Müller)	—	—	—	0.64	0.38	0.02	—	0.31	—	0.24
Retinella electrina (Gould)	—	—	—	0.14	0.10	0.04	—	0.25	—	0.30
Hawaiia minuscula (Binney)	0.29	5.06	—	16.86	16.65	8.48	23.37	3.10	7.29	6.47
Zonitoides arboreus (Say)	0.04	—	—	0.14	0.12	0.02	0.93	0.62	—	0.70
Stenotrema leai (Binney)	0.05	—	—	2.02	1.84	0.02	27.10	0.02	—	—
Sphaerium lacustre (Müller)	—	—	—	—	—	—	—	—	—	0.03
S. occidentale Prime	—	—	—	—	—	—	—	0.19	—	X
S. partumeium (Say)	—	—	—	0.22	—	—	—	0.05	—	—
S. rhomboideum (Say)	—	—	—	—	—	—	—	—	—	X
S. striatinum (Lamarck)	0.04	—	—	—	—	—	—	0.02	—	0.04
S. sulcatum (Lamarck)	—	—	—	—	—	—	—	0.45	—	0.15
S. transversum (Say)	X	—	—	—	—	—	—	—	—	—
Pisidium casertanum (Poli)	0.02	—	—	4.21	—	0.15	0.93	41.15	—	1.69
P. compressum Prime	0.52	—	—	—	—	—	—	1.69	1.46	3.08
P. ferrugineum Prime	—	—	—	—	—	—	—	—	0.05	—
P. lilljeborgi Clessin	—	—	—	—	—	—	—	—	0.29	—
P. nitidum Jenyns	0.16	—	—	—	—	—	—	0.31	0.41	0.91
P. obtusale Pfeiffer	—	—	—	—	—	—	—	0.45	—	0.18
P. subtruncatum Malm	—	—	—	—	—	—	—	—	—	X
P. variabile Prime	—	—	—	—	—	—	—	—	—	0.03
P. walkeri Sterki	X	—	—	—	—	—	—	0.12	12.68	X
Anodonta grandis Say	X	—	—	—	—	—	—	0.03	—	—
Uniomerus tetralasmus (Say)	—	—	—	—	—	—	—	—	—	X
Quadrula quadrula (Rafinesque)	—	—	100.0	—	—	—	—	—	—	—

TABLE V

Relation of Terrestrial to Aquatic Species in Five Late Pleistocene Molluscan Faunas

	Butler Spring local fauna			Cragin Quarry local fauna				Jinglebob l. f.	Jones l. f.	UM-K4–53 faunule
	loc. 1	loc. 2	loc. 3	loc. 1	loc. 2	loc. 3	loc. 4			
Total Number	140,077	336	1	28,472	107	4,720	12,076	6,461	2,059	35,555
Total Number Aquatics	135,428	134	1	14,393	4	73	3,382	4,286	1,420	21,885
Total Number Terrestrials	4,649	202	0	14,079	103	4,647	8,694	2,175	639	13,670
Per Cent (%) Aquatics	96.68	39.88	100	50.55	3.74	1.73	28.01	66.34	68.94	61.55
Per Cent (%) Terrestrials	3.32	60.12	—	49.45	96.27	98.45	71.99	33.66	31.03	38.43

TABLE VI

Species Shared in Common by Five Late Pleistocene Molluscan Faunas

The number listed in the left of each column represents the number of species shared in common. The percentage on the right of each column represents the percentage of species shared in common

	UM-K4-53 faunule		Butler Spring local fauna		Cragin Quarry local fauna		Jinglebob local fauna		Jones local fauna	
UM-K4-53 faunule (54)	—	—	38	70.3%	28	51.8%	44	81.4%	21	38.8%
Butler Spring l. f. (53)	38	71.6%	—	—	27	50.9%	37	66.0%	21	39.6%
Cragin Quarry l. f. (35)	28	79.9%	27	77.1%	—	—	29	82.8%	16	45.7%
Jinglebob l. f. (52)	44	84.6%	37	71.1%	29	55.7%	—	—	22	45.7%
Jones l. f. (28)	21	75.0%	21	75.0%	16	57.1%	22	78.5%	—	—

blages representing different ecologic situations. (3) Collecting methods which treat an entire fossiliferous zone as one unit might tend to obliterate subtle differences which would only be revealed if smaller sample units were taken.

Our present knowledge concerning the factors determining the composition of fossil molluscan faunas is still too limited to permit correlation on the basis of these assemblages alone. Perhaps future

work on the range of variation of individual species taken from faunas of different ages will reveal slight differences through time that may prove to be of some stratigraphic significance. At present, mollusks can best be used for interpreting local environment and as indicators of climatic conditions.

Conclusions

A new Pleistocene molluscan faunule from the Big Springs Ranch, Meade County, Kansas, is described. The 53 species in the faunule are believed to be Illinoian in age on the basis of stratigraphic and paleontologic evidence. If future work can definitely establish the age of the fossils as Illinoian, the term "Butler Spring local fauna" should be used for this local faunule. The assemblage is interpreted as representing three major habitats: (1) a small permanent stream, of the same approximate size as the present Spring Creek; (2) a temporary water situation, perhaps a slough or temporary pond, situated on the flood plain of the stream; and (3) a woodland habitat, situated near the stream.

Most of the species present in this faunule are now found distributed in the central and eastern part of the South Dakota-Nebraska border region. The climatic conditions inferred for the time the mollusks lived are similar to those now prevailing in this area. The postulated climatic conditions for this part of the Illinoian are normal summer temperatures that ranged between 70° and 75° F. and a normal winter temperature of between 15° and 25° F. The normal annual precipitation was between 20 to 30 inches, 40 to 50 per cent of which fell during the summer months.

An analysis of five late Pleistocene molluscan faunas, that ranged in age from Illinoian to Wisconsin, failed to reveal any specific relationships that might be of use in stratigraphic correlation.

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LITERATURE CITED

Baker, F. C. 1928a. The Fresh Water Mollusca of Wisconsin, Part I. Gastropoda. Wisconsin Geol. Nat. Hist. Survey Bull., 70 (Pt. 1): 1–507, 28 pls., 202 figs.

—— 1928b. *Ibid.*, Part II. Pelecypoda. *Id.* (Pt. 2): 1–495, 76 pls., 96 figs.

Goodrich, C. 1940. Mollusks of a Kansas Pleistocene Deposit. Nautilus, 53(3): 77–79.

Herrington, H. B. In press. A Revision of the Sphaeriidae of North America (Mollusca: Pelecypoda). Univ. Mich. Mus. Zool., Misc. Publ.

—— and D. W. Taylor. 1958. Pliocene and Pleistocene Sphaeriidae (Pelecypoda) from the Central United States. Univ. Mich. Mus. Zool., Occ. Pap., 596: 1–28, 1 pl., 2 tab.

Hibbard, C. W. 1949a. Pleistocene Stratigraphy and Paleontology of Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 7(4): 63–90, 1 pl., 2 figs., 3 maps.

—— 1949b. Techniques of Collecting Microvertebrate Fossils. Univ. Mich. Mus. Pal., Contrib., 8(2): 7–19, 4 pls.

—— and D. W. Taylor. 1960. Two Late Pleistocene Faunas from Southwest Kansas. Univ. Mich. Mus. Pal., Contrib., 16(1): 1–223, 16 pls., 18 figs.

Jones, D. T. 1932. Mollusks in the Vicinity of Yankton, South Dakota. Nautilus, 45(4): 115–118.

Leonard, A. B. 1959. Handbook of Gastropods in Kansas. Univ. Kan. Mus. Nat. Hist., Misc. Pub., 20: 1–224, 11 pls., 87 figs.

Over, W. H. 1915. Mollusca of South Dakota. Nautilus, 29(8): 90–95.

Pilsbry, H. A. 1946. Land Mollusca of North America (North of Mexico). Acad. Nat. Sci. Phila. Monog., No. 3, 2(1): 1–520, 281 figs.

—— 1948. *Id. Ibid.*, 2(2): 521–1113, 585 figs.

ROSCOE, E. J. 1954. Terrestrial Gastropods from the Black Hills, South Dakota. Utah Acad. Sci., Arts, and Letters, Proc., 31: 67–72, 1 tab.

—— 1955. Additional South Dakota Terrestrial Gastropod Records. Amer. Mid. Nat., 54(2): 511–512.

SIMPSON, C. T. 1914. A Descriptive Catalogue of the Naiades or Pearly Fresh-Water Mussels. Bryant Walker, Detroit, Michigan, 1–1540.

STARRETT, A. 1956. Pleistocene Mammals of the Berends Fauna of Oklahoma. Jour. Paleont., 30(5): 1187–1192, 1 fig.

TAYLOR, D. W. 1960. Late Cenozoic Molluscan Faunas from the High Plains. U. S. Geol. Surv. Prof. Paper No. 337: 1–94, 4 pls.

VAN DER SCHALIE, H. 1953. Mollusks from an Interglacial Deposit (Sangamon ? Age) in Meade County, Kansas. Nautilus, 66(3): 80–90.

VISHER, S. S. 1954. Climatic Atlas of the United States. Harvard University Press, Cambridge, Mass., 1–403, 1,031 maps and graphs.

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THE MAMMALS OF THE CUDAHY FAUNA

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The Cudahy fauna may prove to be the best possible index to the effects of Pleistocene glaciation on animal distribution and climatic zonation. This important fauna was recovered from silts lying just below the Pearlette ash—the most significant, widespread time-marker in Pleistocene deposits of nonglaciated areas in the Great Plains and Rocky Mountain regions of North America. This volcanic ash is petrographically distinct and is known to occur in an area extending northward from El Paso, Texas, to southern South Dakota, and westward from western Iowa and Missouri to Colorado, Utah, and possibly Las Vegas, Nevada (Swineford, 1949; Powers et al., 1958; Eardley and Gvosdetsky, 1959). Members of the Cudahy fauna are known from pre-Pearlette ash deposits in Texas, Oklahoma, Kansas, and Nebraska. When these widely separated, contemporaneous deposits are adequately sampled, a relatively precise picture of late Kansan animal distribution and climatic zonation can be constructed.

Several reports have been published on the Cudahy fauna. Smith (1938) first reported the presence of vertebrates from under the ash. Hibbard (1944, 1949b) reported the mammals of the fauna and discussed the climatic conditions which probably existed at the time of their deposition. He concluded that the habitats of the nearest living relatives of certain Cudahy mammals indicated a climate considerably cooler and more humid than presently found in southwestern and central Kansas, and that the fauna was of a late glacial age. Subsequent work (Hibbard, 1949b, 1956; Frye and Leonard, 1952) has substantiated this conclusion. Tihen (1955, p. 240) commented on the ambystomid salamanders from the deposit, and the mollusks were recorded by Franzen (1946), Franzen and Leonard (1947), Frye and Leonard, (1952), Leonard (1946, 1948, and 1950), and Johnston and Savage (1955).

The present study is based on material obtained by a University of Michigan Museum of Paleontology field party in the summer of 1958. The party collected most of the material from below the Pearl-

ette ash at the type locality (University of Kansas Locality 10), Cudahy ash mine, SW¼ Sec. 2, T. 31 S., R. 28 W., Meade County, Kansas. A few specimens were obtained from the Sunbrite ash mine (University of Kansas Locality 17), NW¼, SE¼ Sec. 26, T. 32 S., R. 28 W., in Meade County. Remains of 1,089 individuals representing 28 mammalian species were recovered from a zone within 18 inches of the bottom of the ash bed. Twelve of these mammals are new to the original faunal list of Hibbard (1944). Two forms have been described as new species. The additional material has necessitated some taxonomic changes and has allowed for more detailed descriptions, including an analysis of variation within each species with an adequate sample size. In the following taxonomic accounts, the letters UMMZ stand for the University of Michigan Museum of Zoology. All other numbers are those of the University of Michigan Museum of Paleontology.

CLASS MAMMALIA

ORDER INSECTIVORA

Family Soricidae

Sorex cinereus Kerr

Material.—No. 38436, a complete left lower jaw with I, P_4-M_3; Nos. 38437-38439, 39631, 39632, 69 incomplete, tooth-bearing lower jaws. At least 37 individuals are present.

Description.—The lower jaw and teeth are generally more robust than normal for Recent *Sorex cinereus*, but size overlap does occur. The posterior face of the condylar process is very small and is narrowly constricted by a deep lingual depression between the articular facets. The size and configuration of this process appears to be subject to relatively little individual variation. The height of the ascending ramus is subequal to the length of the molar series. The anteroposterior length from the tip of the incisor to the tip of the condyle is 9.2 mm. (1 specimen).

Sorex (*Sorex*) *cudahyensis* Hibbard

(Fig. 1)

Material.—There are 13 lower jaw fragments, 6 of which bear teeth; Nos. 36804, 36805, 39627, 39628, 39634, and 39635. At least 6 individuals are represented.

Description.—*Sorex cudahyensis* is a small shrew with a robust ramus, an elongate molar series, and relatively narrow teeth (Fig. 1). The body of the

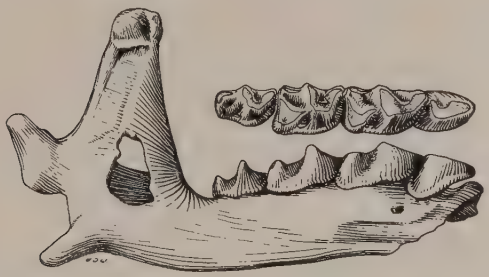

FIG. 1. *Sorex* (*Sorex*) *cudahyensis* Hibbard, No. 39627, right lower jaw with $P_{\bar{4}}$–$M_{\bar{3}}$, labial and occlusal views, × 10.

ramus and the length of the tooth row are but slightly smaller than those of small *S. arcticus laricorum* Jackson, but the part of the ramus posterior to $M_{\bar{3}}$ is 20 per cent shorter and the condylar process is about 30 per cent smaller than that of *S. arcticus*. A mandibular and a postmandibular foramen are present. They are subequal in size and are contained in an elongate, diagonal fossa posteriorly. The infracondylar notch is square. The supracondylar notch, labial muscle scars of the coronoid process, and the posterointernal ramal fossa (Gaughran, 1954) are comparable to those of *S. arcticus* and *S. tundrensis* Merriam. The mental foramen is situated below the metaconid of $M_{\bar{1}}$.

The nature of the incisor cusplets is unknown. Labially, the incisor extends just posterior to the canine. The principal cusp of the canine of No. 39634 lacks the well-pronounced posterior (occasionally lingual) depression of Recent species of the genus *Sorex*. The principal cusp of $P_{\bar{4}}$ is robust, and there is no well-developed ridge on its anterior face. Unlike the holotype, there is a lingual depression posterior to the principal cusp, but it is not as broad or deep as in Recent species of *Sorex*. This depression is in a posterior position in the holotype. The posterolabial cusp is not distinctly set off from the principal cusp in the holotype or in the topotypes; it appears to be in a more medial position. The talonid of $M_{\bar{3}}$ is reduced.

Measurements in mm.—Occlusal length of $M_{\bar{1}}$–$M_{\bar{3}}$, 3.5 (3.4–3.6), 3 specimens. Occlusal length of $M_{\bar{1}}$, 1.38 (1.3–1.4); width of $M_{\bar{1}}$, 0.8, 4 specimens each. Height of ascending ramus, 3.8 (3.6–4.0), 7 specimens. Length of ramus posterior to $M_{\bar{3}}$, 3.2, 1 specimen.

Discussion.—The diagnostic characters for *Sorex cudahyensis* are: (1) a relatively large, uncrested canine and $P_{\bar{4}}$; (2) the presence of a postmandibular foramen; (3) an elongate and narrow molar series; (4) a compact ramus posterior to $M_{\bar{3}}$; (5) a small condylar process.

The presence of a postmandibular foramen excludes most species of the genus *Sorex*. *S. trowbridgi* Baird, *S. vagrans* Baird, *S. obscurus* Merriam, and *S. saussurei* Merriam have a wider tooth row, a well-developed talonid on $M_{\bar{3}}$, and a distinct crest on the anterior face of the canine and $P_{\bar{4}}$. The square infracondylar notch, the proportions of the body of the ramus, the nature of the

muscle scars, and the general dental features of *S. cudahyensis* strongly suggest affinities with the *S. arcticus* group. However, the small size of the condylar process and the compactness of the ramus posterior to M_3 are distinct from those of *S. arcticus*. I am unable to assign *Sorex cudahyensis* to any Recent species group of shrews.

Sorex (*Sorex*) *lacustris* (Hibbard)

(Fig. 2)

Neosorex lacustris Hibbard, 1944, Geol. Soc. Amer. Bull., 55: 721, fig. 5.
Sorex (*Neosorex*) *lacustris* (Hibbard), 1959, PMASAL, 43 (1958): 12.

Material.—There are 39 lower jaw fragments, 26 of which have teeth; Nos. 38358–38363, 39633, 39637, and 42342. At least 15 individuals are represented in the collection.

Description.—The size of the ramus and dentition are slightly smaller than those of *Sorex bendirii albiventer* Merriam. The part of the ramus which is posterior to M_3 (dorsal view) is not as abruptly arched laterally as the ramus of *Neosorex*. Two large posterolingual foramina are contained within an elongate, diagonal fossa posteriorly. The anterior foramen enters the mandibular canal and the posterior foramen enters the floor of the posterointernal ramal fossa (Fig. 2*A*). The infracondylar notch is rather square, but in some specimens it is rounded anteriorly. The column connecting the dorsal and ventral articular facets of the condylar process is not concave lingually (Fig. 2*C*). The posterointernal ramal fossa is large; it is often truncated dorsally by a bony ridge, in which case, a shallow fossette is present. The supracondylar notch and the labial muscle scars of the coronoid process are like those of *S. arcticus* Kerr. The body of the ramus is arched dorsally under M_2. The mental foramen is situated below the protoconid of M_1.

The incisor is robust; has 3 heavy, distinct dorsal cusplets; extends labially to a position just posterior to the canine. The canine and P_4 are relatively large and generalized. The lingual (posterior in some cases) depression posterior to the principal cusp is poorly developed; it is barely evident in the canine of No. 38360. The principal cusp of both the canine and P_4 are better developed than those observed in species of Recent *Sorex*. There is no distinct anterior ridge or terminal cusplet present on the canine or P_4 of *S. lacustris*.

The entoconid of M_1 and that of M_2 are well developed and are joined to their respective metaconids by relatively strong lophids. The paraconid generally has an anteriorly bent crest on its anterior face. The paraconid crest extends down the anterior face of the tooth and overhangs or interrupts the strong anterior cingulum. The labial and the lingual cingulum are like those of *S. arcticus*. The length of the tooth row is approximately 15 per cent longer than that of Recent *Sorex* possessing a postmandibular foramen.

Measurements in mm.—Occlusal length of M_1–M_3, 4.3, 2 specimens. Occlusal length of M_1, 1.64 (1.6–1.7); width of talonid of M_1, 0.92 (0.8–1.0), 7 specimens. Height of ascending ramus, 5.0 (4.8–5.1), 7 specimens.

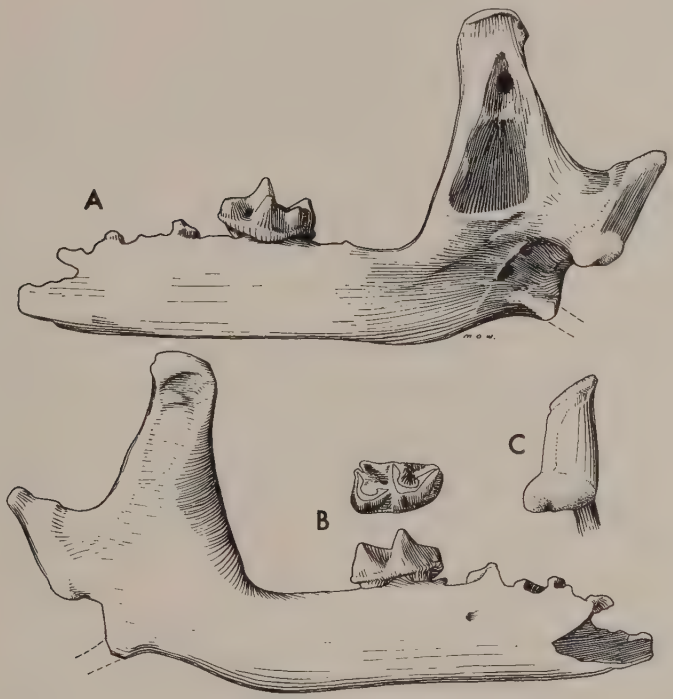

FIG. 2. *Sorex* (*Sorex*) *lacustris* (Hibbard), with $M_{\bar{3}}$, No. 38363, *A*, right jaw with $M_{\bar{3}}$, lingual view showing mandibular and postmandibular foramina; *B*, labial and occlusal views; *C*, posterior view of condyle, all × 10.

Discussion.—Stephens (1960, in press) removed this species from the subgenus *Neosorex* because of the presence of a postmandibular foramen. He considered it to be related to the *Sorex arcticus* group. The absence of a distinct anterior crest on the canine and $P_{\bar{4}}$, the well-developed cusplets of the incisor, the relatively strong lophid joining the entoconid and metaconid, and the less-pronounced curvature (dorsal view) of the ramus between $M_{\bar{3}}$ and the dorsal articular facet, further distinguish *S. lacustris* from *Neosorex*. In these characters, as well as in the nature of the condylar process and infracondylar notch, *S. lacustris* closely approaches the *S. arcticus* condition. I agree with Stephens' contention that its affinities are with the *S. arcticus* group.

Sorex lacustris is distinguished from all Recent *Sorex* that have a postmandibular foramen, by its large size and generalized $P_{\bar{4}}$.

Sorex (Neosorex) megapalustris sp. nov.

(Fig. 3)

Material.—Holotype: No. 38357, an incomplete left lower jaw with $M_{\bar{1}}$–$M_{\bar{3}}$ and a complete ascending ramus. The body of the ramus anterior to $M_{\bar{1}}$ is missing and the teeth are heavily worn. Paratypes: No. 36803 includes 5 lower jaw fragments without teeth and 3 fragments with teeth. At least 4 individuals are represented.

Horizon and type locality.—Pleistocene (late Kansan), Crooked Creek formation, Atwater member; University of Kansas Locality 10 (Cudahy ash mine), SW¼ Sec. 2, T.31 S., R.28 W., Meade County, Kansas.

Diagnosis.—A water shrew with a more robust ramus and larger teeth than those of Recent *Neosorex*. Length of tooth row, width of $M_{\bar{1}}$, and height of ascending ramus, are 8 to 15 per cent larger than large Recent individuals of the subgenus. $P_{\bar{4}}$ is more generalized and not as reduced. The supracondylar notch is more broadly rounded.

Description of holotype.—The holotype is similar to *Sorex bendirii palmeri* Merriam in ramus and tooth size, but the salient characters are those of the subgenus *Neosorex*. The ramus posterior to $M_{\bar{3}}$ is markedly arched labially and the vertical axis of the ascending ramus intersects the body axis at a low angle. There is no postmandibular foramen. The dorsal part of the coronoid process is strongly inclined anteriorly and the muscle scars of its dorsolateral side are comparable to those of *Neosorex* (Fig. 3.1). Although the ventromedial muscle scar of the holotype is in the form of a diagonal ridge, the paratypes indicate that a tubercular scar similar to that in Recent *Neosorex* is the normal con-

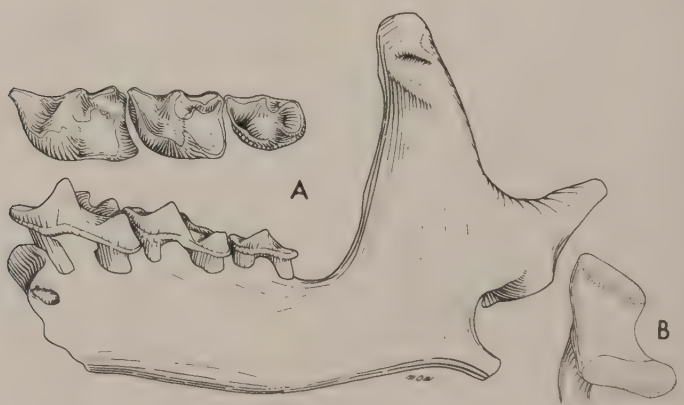

FIG. 3. *Sorex* (*Neosorex*) *megapalustris* sp. nov., holotype, left jaw with $M_{\bar{1}}$–$M_{\bar{3}}$, No. 38357; *A*, labial and occlusal views; *B*, posterior view of condyle, all × 10.

dition. The articular facets of the condylar process are like those of Recent species of *Neosorex*, but the supra- and infracondylar notches are more broadly rounded (Fig. 3*B*). The infracondylar notch of the holotype is 20 per cent wider than that of Recent *Neosorex*. The body of the ramus is arched dorsally below $M_{\bar{2}}$. The mental foramen is placed like that of *Sorex palustris* Richardson but is about twice as large.

The molars of the holotype are extremely large and heavy. $M_{\bar{1}}$ is approximately 15 per cent longer and 20 per cent wider than the largest specimen of *Sorex palustris* observed. The extreme width of $M_{\bar{1}}$ is largely due to the peculiar orientation of the entoconid. This cusp is obliquely inclined beyond the lingual margin of the tooth. The lingual cingulum of $M_{\bar{1}}$ is arched and broadened dorsally just anterior to the metaconid; the labial cingulum is arched dorsally below the protoconid. $M_{\bar{1}}$ is tilted and offset lingually with respect to the position of $M_{\bar{2}}$ and $M_{\bar{3}}$.

Description of paratypes.—The paratype material indicates that the holotype is larger than usual for the species, and that certain characters are a product of old age and heavy wear. The entoconids of the paratypes are not sharply inclined beyond the lingual border of $M_{\bar{1}}$; they are subvertical. The lingual tilt and offset of $M_{\bar{1}}$ in the holotype is a feature of wear. Apparently, as $M_{\bar{1}}$ is worn, new masticatory stresses are introduced and, in response to the new stresses, the tooth is realigned in its alveoli. This interpretation is substantiated by the observation that the identical condition may be observed in old Recent individuals of *S. palustris*.

Like *Sorex palustris*, $P_{\bar{4}}$'s of the paratypes have a strong, narrow crest on their anterior faces. However, the tooth is wider relative to its length than is *S. palustris*. The nature of the canine and incisor is unknown.

Measurements in mm.—Occlusal length of $M_{\bar{1}}$-$M_{\bar{3}}$ in 2 specimens is 4.5. Occlusal length of $M_{\bar{1}}$, 1.82 (1.8–1.85), 4 specimens. Occlusal width of $M_{\bar{1}}$, 1.12 (1.1–1.2), 4 specimens. Height of the ascending ramus, 5.4 (5.3–5.5), 4 specimens.

Discussion.—*Sorex megapalustris* is distinctive in its large size, broadly rounded supracondylar notch, and large $P_{\bar{4}}$. In other characters, however, it is like *S. palustris*. I believe that they are directly related. This is the earliest recorded occurrence of the subgenus *Neosorex*.

Microsorex pratensis Hibbard

Material.—No. 39629, a left lower jaw with I, $M_{\bar{1}}$–$M_{\bar{3}}$; Nos. 39630 and 39636, 10 incomplete lower jaws, 9 of which bear teeth. At least 6 individuals are present.

Description.—The ramus and dentition are very heavy, and the supracondylar notch is broadly rounded. A well-developed depression is present on the axis of the ramus just anterior to the condylar process. The incisor has 2 well-defined tubercles and a suggestion of a third anterior to these. The incisor extends posterolabially to the anterior border of $M_{\bar{1}}$. Ramal body, coronoid and angular processes, infracondylar notch, foramina, dental pattern, and posterointernal ramal fossa are like those of the Recent species (except in size). The posterior face of the articular process is large, but it is overlapped in size

by large Recent individuals. A single mandibular foramen is present. Viewed dorsally, the lingual side of the ramus posterior to M_3 is arched abruptly labiad. This feature serves to separate this form from that of the other small shrews (*Sorex cinereus* and *S. cudahyensis*) of the Cudahy fauna. Height of the ascending ramus averages longer than the length of M_1–M_3.

Measurements in mm.—Anteroposterior length from tip of incisor to tip of condyle, 9.2, 1 specimen. Length of M_1–M_3, 3.2, 2 specimens. Height of ascending ramus, 3.36 (3.3–3.4), 7 specimens.

Discussion.—*Microsorex pratensis* is distinguished from the Recent species by its large size and heavy dentition and by its broadly rounded supracondylar notch. This species appears to be in, or very near to, the ancestral stock from which *M. hoyi* was derived. I have not compared this species with *M. minutus* Brown, of the Conard fissure.

Blarina sp.

Material.—No. 36802, a fragment of a left jaw with M_1 and M_2; ascending ramus and body of ramus anterior to M_1 is missing. Teeth are well worn.

Description.—The molars average larger than those of large subspecies of *Blarina brevicauda* Say, but an overlap of size does occur. The mental foramen is surrounded by a pronounced depression and is situated below the paraconid of M_1. The metaconid and entoconid of M_1 and M_2 are not joined by lophids. The above features agree with those of *B. brevicauda*. The lingual cingulum of M_2 is better developed than that of the Recent species. The occlusal length of M_1 to M_2 is 3.8 mm. The greatest width of M_1 is 1.4 mm. The specimen is too fragmentary for specific determination.

ORDER CARNIVORA

The remains of carnivores are rare in the deposit. Those specimens which were recovered are being reported on by Lowell Getz (1960). Parts of *Canis* sp., *Mustela* cf. *erminea* Linnaeus, and *Mustela* cf. *vison* Schreber were identified by Getz.

ORDER RODENTIA

Family Sciuridae

Citellus richardsoni (Sabine)

(Fig. 4*E*)

Material.—No. 36796, 28 isolated teeth. No. 39578, a maxillary fragment with 2 heavily worn teeth. No. 39579, a left jaw with M_1 and M_2 and alveoli for P_4 and M_3. No. 39588, a badly eroded right jaw with P_4 and M_1. At least 3 individuals are represented.

Description.—No. 39579 (Fig. 4*E*) is indistinguishable from the mandible of *Citellus richardsoni*. The anterior vertical prominence of the masseteric scar of *C. armatus* (Kennicott) is distinctive from that of the fossil material. The mental foramen is placed as in Recent *C. richardsoni*, and the muscle scar

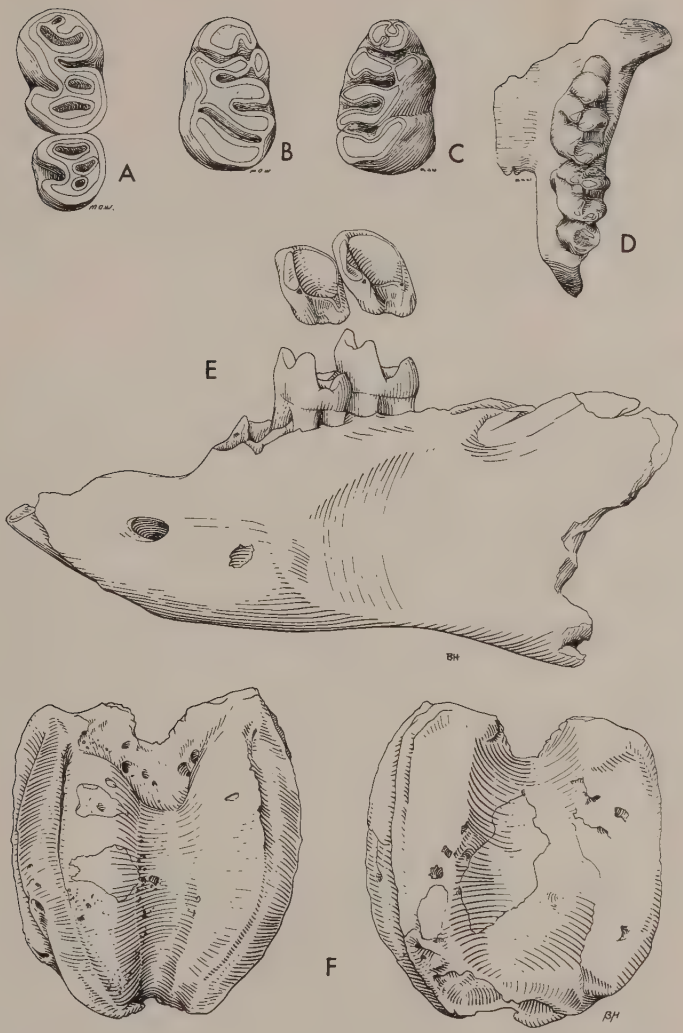

FIG. 4. *A–C*, *Zapus* cf. *sandersi* Hibbard; *A*, No. 38343, left $M_{\bar{2}}$ and $M_{\bar{3}}$, occlusal view; *B*, No. 38342, left $M_{\bar{1}}$, occlusal view; *C*, No. 39518, right $M_{\bar{1}}$, occlusal view, all × 16; *D*, *Reithrodontomys moorei* (Hibbard), No. 39520, left $M^{\underline{1}}$–$M^{\underline{3}}$, occlusal view, × 10; *E*, *Citellus richardsoni* (Sabine), No. 39579, left jaw with $M_{\bar{1}}$ and $M_{\bar{2}}$, labial and occlusal views, × 5; *F*, *Megalonyx* sp., No. 38404, second metacarpal of fourth digit, distal and proximal views, × 1.

on the anterolingual border of $P_{\bar{4}}$ is similar in depth and position. The alveolar length of $P_{\bar{4}}$–$M_{\bar{3}}$ is 9.2 mm.; the depth of jaw below $M_{\bar{1}}$ is 6.5 mm., and the length of $M_{\bar{1}}$–$M_{\bar{3}}$ is 6.5 mm. The upper teeth and the anterior lower teeth are inseparable from those of *C. richardsoni*. One $M_{\bar{3}}$ assigned to this species duplicates the $M_{\bar{3}}$ of smaller individuals of *C. richardsoni*, but all other third molars assigned to this species are smaller and tend to have a less rugose basin and a more narrow talonid. My assignment of these teeth to *C. richardsoni* may be questioned, however.

Citellus cf. *tridecemlineatus* (Mitchill)

Material.—No. 39577, a fragment of a lower jaw with heavily worn $M_{\bar{1}}$ and $M_{\bar{2}}$; No. 42320, 40 isolated teeth. At least 4 individuals are present.

Description.—The size of the teeth corresponds closely with those observed in large individuals of *Citellus tridecemlineatus arenicola* Howell. I was unable to detect any significant differences between the upper cheek teeth of the fossil material and those of Recent specimens. The cone-shaped metaconules of M^1 and M^2 are well developed and separate from the slightly compressed protocones. The parastyle is well developed and its continuation (anterior cingulum) gradually converges posteriorly toward the protocone, where it ends with an abrupt bend. The slight indentations on the outer wall of the well-developed talon of M^3 and the very small, but distinct, elongate enamel fold (metaloph or metacone or both) are common to both fossil and Recent specimens.

Although some of the fossil lower cheek teeth assigned to this species are slightly more compressed anteroposteriorly than in most Recent individuals, there is considerable correspondence in detail. The only difference of possible specific significance is found in the development of the slight groove extending anteriorly from between the hypoconid and entoconid of $M_{\bar{3}}$. This groove is deeper and wider than that of Recent specimens examined. However, the talonid and its basin are subject to such variation in the Recent species, that I am inclined to disregard the difference until more adequate material is obtained.

Citellus nr. *franklini* (Sabine)

Material.—No. 39596, maxillary fragment with RM^1 and M^2; No. 42319, 26 isolated teeth. At least 2 individuals are represented.

Description.—As in the Recent species, the upper molariform teeth possess a well-developed, anteroposteriorly compressed metaconule, united to the metacone by a relatively weak metaloph and connected to the protocone at its base. The mesostyle is variable in size but present in the broadly rounded central valley, which is relatively deep but not so deep as the anterior or posterior valleys. The paracone is better developed than the metacone but is not so high as the anteriorly inclined protocone. The height of crown is equal to that of the Recent species. The characteristic notch just posterior to the protocone of M^2 is present in both forms.

Although the $M_{\bar{3}}$ assigned to this form agrees with that of *Citellus franklini* in most details of dental topography, its general shape is distinct. The postero-

lingual part is narrow and imparts a triangular appearance to the fossil tooth. The M_3 of *C. franklini* is more squared in appearance. I could not detect any characteristic differences between the anterior lower cheek teeth of the Cudahy material and those of Recent *C. franklini*.

Discussion.—If I am correct in believing that the third lower molars belong with the other dental elements referred to *Citellus* nr. *franklini*, then these specimens probably represent a new species. Such a designation, however, must be held in abeyance until associated material is collected.

Family Geomyidae

Thomomys sp.

Material.—No. 42317, a fragmentary ramus with P_4; an isolated P^4 and 5 molar teeth.

Description.—The generic designation is based on the presence of enamel on the posterior face of P^4 and on the anterior faces of the lower molars. The upper molars are strongly constricted labially and the lowers lingually. Two molars have a third enamel band on the unconstricted side. The dentine tracts of the anterior column of P^4 are situated as those on the P^4 of *T. umbrinus* (Richardson). The lingual dentine tract is wider than the labial. The internal wall of the anterior column of P_4 is concave, and the enamel plate does not extend to the anterior face. The ventral masseteric scar is strongly developed.

Measurements in mm.—Depth of jaw below P_4, 5.7. Occlusal length of P_4, 2.0; width of anterior column, 1.3; width of posterior column, 1.5. Occlusal length of P^4, 1.6; width of anterior column, 1.0; width of posterior column, 1.4.

Discussion.—The material on hand indicates that it is distinct from *T. gidleyi* Wilson, but it is inadequate for specific determination.

Geomys tobinensis (Hibbard)

Parageomys tobinensis Hibbard, 1944, Geol. Soc. Amer. Bull., 55: 735, fig. 16.
Geomys (*Parageomys*) *tobinensis* (Hibbard), Hibbard, 1956, PMASAL, 41 (1955): 183, fig. 11.

Material.—Seven incomplete lower jaws with teeth (Nos. 39582, 39585–39587), 2 maxillary fragments (Nos. 39583 and 42316), and numerous isolated teeth. At least 20 individuals are represented.

Diagnosis.—A small *Geomys* which is near the size of *G. bursarius dutcheri* Davis. The anterior part of the masseteric crest is situated above the horizontal midline of the labial side of the ramus. The infraorbital canal is deep and in a more posteroventral position than in Recent *Geomys*. The area of the anterior palatine foramina is very stout. The ventromedial ridge of the palate is not developed anterior to P^4.

Description.—The lower jaw is comparable to *Geomys bursarius dutcheri* in size, but the diastema is longer (8.7 mm.) and the jaw is less curved anteriorly. These features, however, are well within the range of variability of Recent *G. bursarius* as that species is now conceived. The pit situated between M_3 and the ascending ramus is as deep as Recent *Geomys*, but there are

no specimens complete enough to indicate its shape. The mental foramen is medially placed. The anterior part of the masseteric crest is located dorsal to the midline of the labial side. I have observed a similar condition in specimens of *G. b. major* Davis and *G. b. brazensis* Davis, but the usual position of the masseteric crest in Recent *Geomys* is ventral to the midline anteriorly.

The maxillaries in the collection are fragmentary, but No. 39538, an adult, displays some rather important departures from structures found in Recent *Geomys*. The infraorbital canal is situated in a more posteroventral position and is much deeper. The distance from the posterior extremity of the canal to the basal crest of the zygomatic process is 5.5 mm. and the depth of the canal at its posterior extremity is 1.7 mm., or approximately twice that observed in Recent species. The floor of the canal is broadly rounded. The anteroventral part of the maxillary is more robust (not constricted) in *G. tobinensis*. The prominent medial crest which extends along the ventral midline to, or almost to, the anterior palatine foramina in Recent adult *Geomys* is indistinct immediately anterior to P^4 in *G. tobinensis*. I was unable to find a comparable condition in 125 Recent adult specimens.

The enamel folds of P^4 are generally well compressed, but those of young individuals commonly approximate the V-shaped re-entrants of *Thomomys*. The molars are ovate in most adults, but some may have a flat surface on one side (Hibbard, 1944, fig. 7*B*). Both of these occurrences have been observed in the young of *Geomys bursarius*. *G. tobinensis* has an enamel cap on all cheek teeth in youth. With wear, the remnants of these caps appear as continuous, closed, enamel bands on the occlusal surfaces. It is only with continued wear that the charactertistic enamel patterns of the genus appear. This has also been observed in Recent *Geomys* (Merriam, 1895).

Measurements in mm.—P^4: occlusal length, 2.4 (1.9–2.9); width of anterior column, 1.5 (1.2–1.7); width of posterior column, 2.0 (1.7–2.3); 10 specimens each. P_4 : occlusal length, 1.9 (1.6–2.2); width of anterior column, 1.6 (1.3–1.7); width of posterior column, 1.9 (1.6–2.4); 10 specimens each. The depth of jaw below P_4 of 3 specimens are 8.3, 8.5, and 8.7.

Discussion.—Geomys tobinensis is distinct from the *Geomys* material reported from the Sanders fauna (Hibbard, 1956). Although the lower jaw of the latter is larger and more robust, it has a diastemal length 14 per cent shorter, due to the extreme anterior curvature of the jaw. Furthermore, in the jaws from the Sanders fauna: (1) the ventral muscle scar of the masseteric crest is in a more ventral position; (2) the mental foramen is in a more posteroventral position; (3) the pit between M_3 and the coronoid process is distinctly shallower; (4) the maxillary is strongly constricted anteriorly and the prominent medial crest on its ventral surface extends to the anterior palatine foramina; (5) the infraorbital canal is shallow.

Geomys quinni McGrew is much larger than *G. tobinensis*. The depth of jaw is 40 per cent greater and the incisor width, the diastemal length, and the size of P_4 average over 20 per cent larger. More significantly, the pit labial to M_3 is not as well developed as in *G. tobinensis*.

An interesting, primitive character persists in approximately 5 per cent of the teeth of *Geomys tobinensis*. A thin enamel band may be present on the

posterior face of P^4 and on the anterior face of the lower molars. This band, when present, extends to the base of the tooth and is not, therefore, a character of youth. In a study of 75 specimens of *G. b. dutcheri*, I found but 1 specimen (UMMZ No. 99734) which possessed these atavistic characters. Hibbard (1950, p. 138, fig. 7) reported a similar occurrence on P^4 of *Nerterogeomys* cf. *minor* (Gidley) from the Upper Pliocene Rexroad formation. Although this form cannot be considered to be ancestral to *Geomys*, it is of interest to note that the frequency of occurrence is 43 per cent (75 specimens).

Family Cricetidae

Reithrodontomys moorei (Hibbard)

(Fig. 4*D*)

Cudahyomys moorei Hibbard, 1944, Geol. Soc. Amer. Bull., 55: 725, fig. 9.

Material.—No. 38348, a left lower jaw with I–M_3; the coronoid process is missing, and the teeth are slightly worn. No. 39520, a maxillary fragment with M^1–M^3.

Description.—A small harvest mouse with a ramus slightly smaller than average for that of *Reithrodontomys humulus* (Audubon and Bachman). The position and size of the mental foramen is similar to that of *R. humulus*. The tooth row is narrow relative to its length. M_3 is notably reduced in size.

The anteroconid is simple, conical, and without external or internal folds. The anterolophid is well developed and is united to the protoconid in all teeth; a weak extension of this ridge is continuous with the hypoconid in M_1 and M_2. A small cusplet is developed on the ridge at the labial extreme of the protoconid of M_1 and of M_2. The protoconid of M_1 is weakly developed, rounded, and strongly inclined lingually. In appearance, it is more a low-lying fold than a cone-shaped cusp. The hypoconid of M_1 and M_2 lie in a lingual position and are broadly rounded rather than cone-shaped. The posterior cingulum is short and is not distinctly set off from the hypoconid. The lingual cusps of all teeth are well developed and conical. The anterolingual valley is very shallow and is anteriorly placed. Its labial extension curves abruptly posteriad between the anterolophid and the protoconid, rather than bisecting the labial wall of the tooth. The medial part, if present, is lost with slight wear. The primary folds are broad and rather U-shaped.

M_3 is reduced, narrow, and elongate (about 20 per cent longer than wide). The protoconid is very small, not bulbous. The first primary fold is much more extensive than the major fold, but the valley between the metaconid and the hypoconid is almost completely closed by a strong lophid. The major fold is a mere indentation. The cuspular pattern is C-shaped (Hooper, 1952, p. 29). The cusps are well fused.

The upper molars are hypsodont and with deep, broad, re-entrant folds. The cusps are alternate in position, inclined posteriorly, compressed anteroposteriorly (except hypocone), and united to the succeeding posterior cusp at their posteromedial border (Fig. 4*D*). Accessory lophs and styles are absent. The anterior cingulum is well developed in M^2 and M^3. The hypocone of M^2

is in a more posterior position than normal for *Reithrodontomys montanus* or *R. humulus*. This imparts a squared appearance to the posterior margin of the tooth. M^3 is reduced in size; it has a C-shaped occlusal pattern and is rounded in shape, but it is wider than long. The first primary fold is much shorter than the second primary fold and does not extend to the midline of M^3. The major fold is absent. A fourth root, narrow and anteriorly inclined, is present below the paraconid of M_1. The other 3 roots are in their normal positions. Three roots are present in M^2.

Measurements in mm.—No. 38348: alveolar length of M_1–M_3, 2.9. Length of M_1, 1.4; width, 0.8. Length of M_2, 1.0; width, 0.8. Length of M_3, 0.65; width, 0.55. No. 39520: alveolar length of M^1–M^3, 3.3.

Discussion.—The trenchant characters separating *Reithrodontomys moorei* from all Recent and fossil species are: (1) the anterior position and shallowness of the anterolabial groove on M_1 (if present medially, soon lost with slight wear); (2) the reduced and recumbent nature of the protoconid and, to a lesser extent, the hypoconid of M_1 and M_2; (3) the reduced condition of M_3 in general, and of its protoconid in particular.

The fused and reduced nature of the cusps and valleys of M^3 clearly place *R. moorei* in the *megalotis* group of the subgenus *Reithrodontomys* (Hooper, 1952). More specifically, the presence of a labial shelf on M_1 and M_2 indicate that its morphological affinities are nearest to those of *R. montanus* (Baird), *R. humulus*, and *R. burti* Benson, the only Recent species possessing the shelf. The recumbent nature of the protoconid and hypoconid, the well-developed anterolophid, and the enclosed condition and posterior trend of the labial extension of the anterolingual fold, are most like those of *R. humulus*. On the other hand, the narrow and reduced condition of M_3, the alternate positioning of the upper molar cusps, and the degree of hypsodonty are more like those of *R. montanus* and, presumably, *R. burti*. It is assumed, however, that the reduced and folded nature of the labial cusps of M_1 and M_2, the shallowness of the anterior groove of M_1, and the pronounced reduction of M_3 are advanced characters. If this view is correct, *R. moorei*, although closely related, is too specialized to have given rise to any known member of the genus.

Subsequent to the original description of *Cudahyomys moorei*, Claude W. Hibbard discovered a third root on M_1 of the holotype. In the course of this study, I have observed several specimens of *R. montanus* (Nos. 66950, 79280, 95871 UMMZ) with 3 roots on M_1. X-rays of the topotype (No. 38348), however, show no third root. *R. montanus* and *R. megalotis* also frequently have a fourth root under the paracone of M^1. To my knowledge, the presence of extra roots on M_1^1 has not been previously reported for the genus.

Peromyscus cragini Hibbard

Material.—No. 35919, a left maxillary with M^1; No. 38346, a left jaw fragment with I–M_2; No. 38347, a right jaw with an incisor and M_1. Nos. 39521 and 39576, 2 maxillary fragments with heavily worn teeth. Only 1 individual is definitely represented.

Description.—The remains of this small mouse are rare in the fauna. As observed in the holotype, the lower molars of No. 38346 are simple and display

no accessory lophids or stylids. A thin cingulum connects the protoconid and hypoconid in $M_{\bar{1}}$ and $M_{\bar{2}}$, but there is no indication of cusplet development. The protolophid is short but stout and is not distinct from the anteroconid. $M_{\bar{2}}$ is wider, but not as elongate as that of the holotype. The occlusal length of $M_{\bar{1}}$–$M_{\bar{2}}$ is 2.6 mm.; the alveolar length of $M_{\bar{1}}$–$M_{\bar{3}}$ is 3.4 mm.; the diastemal length is 2.9 mm.; and the depth of jaw below $M_{\bar{1}}$ is 2.6 mm. $M_{\bar{1}}$ of No. 38347 has a small mesostylid between the metaconid and entoconid, and the anterior part is narrower than that of the holotype. They compare well in other features, however. The greatest length of $M_{\bar{1}}$ is 1.4 mm.

Ondatra annectens (Brown)

(Fig. 5)

Ondatra kansasensis Hibbard, 1944, Geol. Soc. Amer. Bull., 55: 721, fig. 5.
O. kansasensis Hibbard, Hibbard, 1958, PMASAL, 43(1957): 12.
O. annectens (Brown), Stephens, 1960, in press.

Material.—Nos. 38334 and 38335, 2 fragmentary jaws with $M_{\bar{1}}$ and $M_{\bar{2}}$, ascending rami are absent. Nos. 38336 and 38337, 34 isolated teeth. No. 42318, a toothless maxillary. At least 4 individuals are represented.

Description.—Because Hibbard (1944, pp. 732–734, fig. 14) has described and illustrated the teeth of this form in considerable detail, little of significance

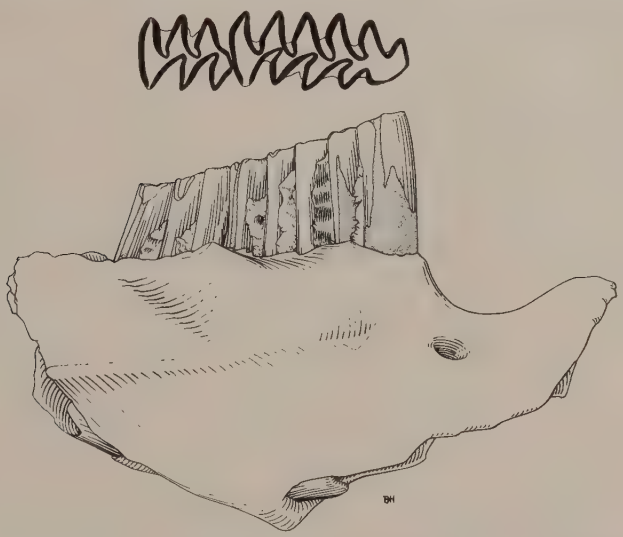

FIG. 5. *Ondatra annectens* (Brown), No. 38335, labial view of right jaw and occlusal view of $M_{\bar{1}}$ and $M_{\bar{2}}$, × 5.

can be added here. The occlusal patterns of M_1 and M_2, as well as the position of the mental foramen and the masseteric crest are illustrated in Fig. 5. The ventral surface of the maxillary displays structures comparable to Recent *Ondatra*. The medial depression is deeper than the lateral palatal grooves. The palatine joins the maxillary at a position similar to that of Recent *Ondatra*.

Measurements in mm.—The occlusal length of M_1 is 5.67 (5.4–6.1), 4 specimens; occlusal width of M_1 is 2.28 (2.1–2.5), 4 specimens.

Discussion.—Stephens, who studied the above material in connection with his study of the Doby Springs local fauna from Oklahoma, compared this material with the holotype of *Ondatra annectens* (Brown). He states: "Better material was recovered in the summer of 1958 of *Ondatra kansasensis* Hibbard, from the Cudahy local fauna of southwestern Kansas. . . . A comparison of this material . . . was made with *Ondatra annectens* (Brown), A.M.N.H. No. 12424 (a left lower jaw and right M^1) from the Conard Fissure, Arkansas. This comparison showed that *O. kansasensis* is the same as *O. annectens*." I have followed Stephens in this assignment.

Synaptomys (Mictomys) meltoni sp. nov.

(Fig. 6)

Material.—Holotype: No. 38327, a left lower jaw with incisor, M_1, and M_2. The posterior part of the ascending ramus is missing. Paratypes: Nos. 38328–38332 include 5 jaw fragments with M_1–M_2, and Nos. 39572 and 39606 include 5 incomplete jaws with M_1. There are 119 isolated teeth in the collection. The minimal number of individuals represented is 39.

Horizon and type locality.—Pleistocene (late Kansan), Crooked Creek formation, Atwater member; Locality 10, Cudahy ash mine, SW¼ Sec. 2, T.31 S., R.28 W., Meade County, Kansas.

Diagnosis.—The size of the ramus is about that of *Synaptomys borealis chapmani* Allen, but the teeth are larger. The enamel of the molars is differentiated into thick and thin portions. In the lower teeth, the enamel of the anterior walls of the triangles is much thicker than that of the posterior walls. In the upper teeth, the enamel of the anterior walls of the triangles is thinner than that of the posterior walls. The first triangle of M_1 has a convex rather than a concave posterior wall, and the base of the second triangle is broad. There is no distinct, cement-filled labial re-entrant on M_3. The basal capsular process for the incisor is situated as in Recent *Mictomys*.

Description of holotype.—The holotype (No. 38327) is a left lower jaw of an adult with incisor, M_1, and M_2 (Fig. 6*C*). M_1 consists of 4 closed prisms; a posterior loop, first and second triangles, and an anterior loop. The posterior wall of the first triangle is convex and the base of the second triangle is broad. The enamel on the posterior walls of the 4 prisms is reduced to a very thin and delicate plate. The enamel of the anterior walls is 2 to 3 times thicker than that of the posterior walls. M_2 consists of 3 closed triangles. The posterior wall of the second triangle is convex. Like M_1, the enamel of the anterior wall is much thicker than the posterior wall. The capsular process for the reception of the base of the incisior is just anterior to M_3.

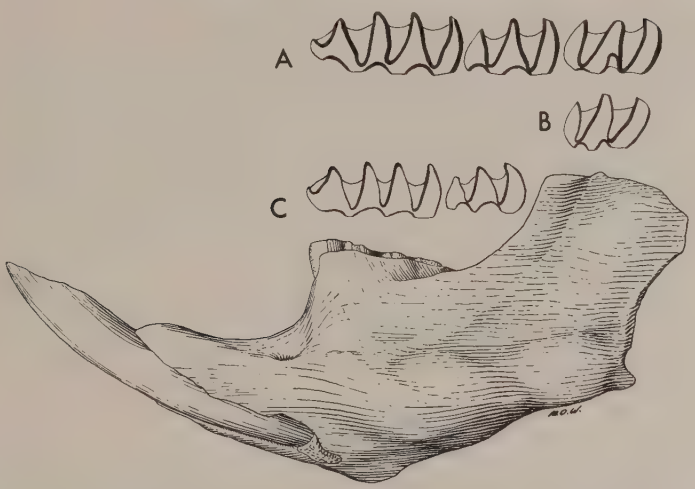

FIG. 6. *Synaptomys* (*Mictomys*);, *A S. borealis* (Richardson), UMMZ No. 97546, occlusal view of $M_{\bar{1}}$–$M_{\bar{3}}$; *B*, *S. meltoni*, sp. nov., $M_{\bar{3}}$, occlusal view; *C*, holotype, *S. meltoni*, sp. nov., $M_{\bar{1}}$ and $M_{\bar{2}}$, labial and occlusal views, all × 8.

Description of paratypes.—The characters of the holotype described above are shared by all paratypes. The rest of this description is based upon isolated teeth.

$M_{\bar{3}}$ is distinctive (Fig. 6*B*). It consists of 3 triangles, 2 lingual re-entrants, and 2 labial crenulations. Unlike Recent *Mictomys*, the second and third triangles have convex posterior walls. The enamel distribution of $M_{\bar{3}}$ is like that of the anterior molars; thick on the anterior walls and thin on the posterior. There is no distinct, cement-filled labial re-entrant. The configuration of the upper molars is the same as in Recent *Mictomys*, but the enamel of the anterior walls of all triangles is reduced.

Measurements in mm.—Holotype: length of diastema is 3.5. Depth of jaw below $M_{\bar{1}}$ is 4.7. Width of incisor is 1.0. Occlusal length of $M_{\bar{1}}$ to $M_{\bar{2}}$ is 4.3. Paratypes: the average and extreme measurements obtained from 13 specimens of $M_{\bar{1}}$ are occlusal length, 2.8 (2.5–3.2); width, 1.1 (1.0–1.2).

Discussion.—*Synaptomys borealis* (Richardson), the only living representative of the subgenus *Mictomys*, is characterized in part by: (1) an equal thickness of enamel on both walls of the prisms (Howell, 1927, p. 8); and (2) deep lingual re-entrants and simple cementless crenulations on the labial side of the lower teeth, with the exception of $M_{\bar{3}}$ in which a distinct, cement-filled re-entrant is developed (Howell, 1927, p. 20). The teeth of *S. meltoni* have an unequal enamel distribution, with no cement-filled, labial re-entrant in $M_{\bar{3}}$ (Fig.

6*B*). In addition, Recent *Mictomys* frequently have a thin, continuous band of enamel around the anterior prisms of $M_{\bar{1}}$, $M_{\bar{2}}$, and $M_{\bar{3}}$, and on the labial side of the posterior prisms of $M_{\bar{2}}$ and $M_{\bar{3}}$. These occurrences are not present in *S. meltoni*. The advanced state of enamel reduction in *Synaptomys meltoni* strongly suggests that it is not ancestral to *S. borealis*.

Synaptomys kansasensis Hibbard is distinct from *S. meltoni* although the similar configuration of the teeth and the comparable state of enamel differentiation establish their close relationship. In *S. kansasensis*, the basal capsular process is situated well posterior to the anterior border of $M_{\bar{3}}$, although it is anterior to $M_{\bar{3}}$ in *S. meltoni*. In addition, the lower jaw of *S. kansasensis* is much larger; $M_{\bar{1}}$ being 11 per cent wider, the incisor 17 per cent wider, and the ramus below $M_{\bar{1}}$ 22 per cent deeper.

This is the earliest recorded occurrence of the subgenus *Mictomys*. It is named for William G. Melton, Preparator at the University of Michigan Museum of Paleontology, who led the field party that recovered the specimens discussed in this report.

Microtus paroperarius Hibbard

(Fig. 7)

Material.—In varying states of completeness, 217 tooth-bearing lower jaws and numerous isolated teeth; Nos. 24715, 38349 38355, 38442, 38443, 39568, 39569, 39574, 39581, 39607–39612, and 42128. A count of lower left $M_{\bar{1}}$'s indicates that at least 723 individuals are represented.

Description.—Normally, $M_{\bar{1}}$ consists of a posterior loop, 4 closed triangles, and a fifth triangle which is open and confluent with the anterior loop. In approximately 20 per cent of the jaws, however, the fourth lingual and the third labial re-entrants converge to close the fifth triangle. The fourth labial re-entrant is normally present and is developed enough to contain cement in more than half of the specimens. I have not observed cement in the fourth labial re-entrants of any of the specimens of *Microtus oeconomus* Pallas—the nearest living relative of *M. paroperarius*—in the collection of the University of Michigan Museum of Zoology. The fifth lingual re-entrant is almost always present and is deeper and better developed than in *M. oeconomus*. In 1 specimen (No. 39569, Fig. 7*G*), a faint suggestion of a sixth lingual re-entrant is present. The variation in the size and depth of the re-entrants mentioned above determines the shape of the anterior loop. Fig. 7*A–G* is designed to demonstrate the gradational nature of the progression from a 4 to a 5 closed-angle condition, as well as to indicate the variable degrees of development of the fourth labial and fifth lingual re-entrants. Fig. 7*C* is the normal condition for $M_{\bar{1}}$ with 4 closed triangles, and Fig. 7*E* is the normal condition for $M_{\bar{1}}$ with 5 closed triangles.

Measurements in mm.—Occlusal length of $M_{\bar{1}}$–$M_{\bar{3}}$, 5.96 (5.4–6.5), 6 specimens. Occlusal length of $M_{\bar{1}}$–$M_{\bar{2}}$, 4.49 (4.1–4.7), 20 specimens. Occlusal length of $M_{\bar{1}}$, 2.96 (2.6–3.4), 20 specimens; width of $M_{\bar{1}}$, 1.07 (1.0–1.2), 20 specimens. Length of diastema, 3.91 (3.3–4.1), 10 specimens. Greatest depth of jaw, 4.87 (4.3–5.5), 10 specimens.

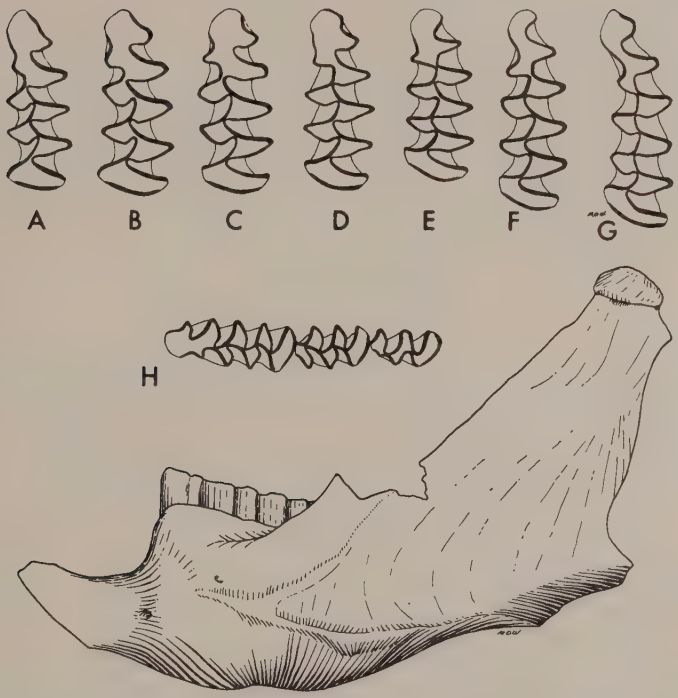

FIG. 7. *Microtus paroperarius* Hibbard, *A–G*, left $M_{\bar{1}}$ variation series, *A* and *B*, No. 36801; *C–F*, No. 36800; *G*, No. 39569; occlusal views, all × 10; *H*, No. 38350, left jaw with $M_{\bar{1}}$–$M_{\bar{3}}$, labial and occlusal views, × 8.

Discussion.—Claude W. Hibbard and I collected a poorly preserved specimen (No. 42128) of *Microtus paroperarius* from a reddish, sandy silt below the Pearlette ash exposure on the ranch of Alfred Shoemaker, SE corner, NW¼, NW¼ Sec. 26, T.19 N., R.13 W., Valley County, Nebraska, in the summer of 1959. In this specimen, the incisor, $M_{\bar{1}}$ and $M_{\bar{2}}$ are present. $M_{\bar{1}}$ consists of a posterior loop, 4 closed angles, and a constricted fifth angle which is confluent with the anterior loop. A broad, fourth labial re-entrant is present. $M_{\bar{2}}$ consists of a posterior loop and 4 closed angles. The occlusal length of $M_{\bar{1}}$ is 2.15 mm., and the width is 0.8 mm. The estimated length of $M_{\bar{1}}$–$M_{\bar{3}}$ is 4.0 mm.

This specimen agrees with the occlusal pattern of *M. paroperarius*, but it is 11 per cent smaller than the average specimen of *M. paroperarius* from the type locality. I believe that its small size is more a result of geographic varia-

tion than of age or individual variation, since the specimens from Russell and Lincoln counties, Kansas, as measured by Hibbard (1944, pp. 737 and 740) are intermediate in size.

The dental pattern of $M_{\bar{1}}$ of *Microtus oeconomus* is usually characterized as having". . . only four closed triangles, (the) fifth triangle being open and confluent with (the) short terminal loop. . ." (Hall and Kelson, 1959, p. 735). In a study of 45 Recent specimens of *M. oeconomus*, I found that 18 per cent had 5 closed angles on $M_{\bar{1}}$. I believe that the similar frequency of occurrence of 5 closed angles in *M. oeconomus* and *M. paroperarius* indicates a relationship between the 2 species. Hibbard (1955, p. 90) considers *Microtus speothen* (Cope) to be related to, but distinct from, *M. paroperarius*.

Pitymys meadensis Hibbard

(Fig. 8*A–G*)

Material.—In various degrees of completeness, 68 tooth-bearing lower jaws and numerous isolated teeth. None of the jaws possesses a complete ascending ramus. Nos. 24714, 27174, 36224, 36799, 38356, 38440, 38441, 39570, 39571, 39595, 39602, 39603. A count of right $M_{\bar{1}}$'s indicates that at least 206 individuals are represented in the collection.

Description.—The characters cited in the original diagnosis (Hibbard, 1944, p. 731) of *Pitymys meadensis* are remarkably constant. In $M_{\bar{1}}$, the dentine of the posterior loop and the first 3 alternating triangles are almost always separate from one another (one exception in 150 teeth); that of the confluent fourth and fifth triangles is consistently separate from the dentine of the anterior loop and of the third triangle. The posterior loop and the 4 triangles of $M_{\bar{2}}$ are also normally closed (Fig. 8*G*).

The fourth labial and fifth lingual re-entrants of the anterior loop are highly variable. Generally, these re-entrants are broad and relatively shallow, but in some cases, they may be so well developed that the dentine of the anterior loop is divided into two separate units. Fig. 8*A–F* illustrates this progression. Both of these re-entrants ordinarily contain cement, but it may be absent from the fourth labial re-entrant in exceptional cases. The angular and broad nature of the labial re-entrants—notably the second—are distinct from the oblique, crescent-shaped re-entrants typical of Recent *Pitymys* and *Pedomys*.

Measurements in mm.—Occlusal length of $M_{\bar{1}}$–$M_{\bar{3}}$, 6.0, 1 specimen. Occlusal length of $M_{\bar{1}}$–$M_{\bar{2}}$, 4.4 (4.1–4.7), 15 specimens. Occlusal length of $M_{\bar{1}}$, 3.0 (2.8–3.3) 10 specimens; width of $M_{\bar{1}}$, 1.15 (1.0–1.2), 20 specimens. Length of diastema, 3.4 (3.0–3.9), 5 specimens.

Discussion.—The enamel pattern, the well-developed fourth and fifth lingual re-entrants of $M_{\bar{1}}$, and the angular nature of the labial re-entrants of $M_{\bar{1}}$ suffice to separate *Pitymys meadensis* from all living and fossil North American species. The $M_{\bar{1}}$ of *P. gregaloides* Hinton (4 specimens, No. 39773) from the upper Biharium (= Kansan) of central Bohemia is 13 per cent smaller and lacks a fourth labial re-entrant. The fifth lingual re-entrant is well developed and the configuration of the labial re-entrants are comparable to those of *P. meadensis*. In *P. hintoni* Kretzoi (No. 34914, 2 specimens), from equivalent

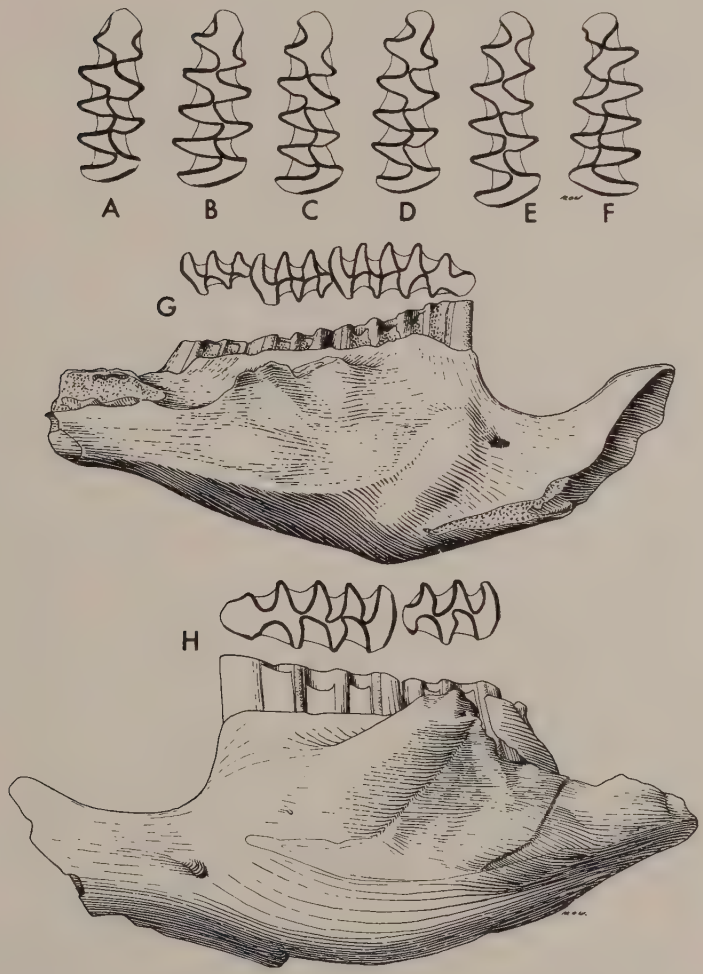

FIG. 8. *A–G, Pitymys meadensis* Hibbard; *A–F*, No. 39571, variation series, five right and one left M_1, occlusal views, all × 10; *G*, No. 38356, labial and occlusal views, × 8; *H, Pedomys llanensis*, No. 39604, labial and occlusal views, × 10.

deposits in Yugoslavia, the fourth labial and fifth lingual re-entrants are not well developed.

Hibbard (1944) pointed out that *Pitymys meadensis* appeared too late to be considered ancestral to Recent North American *Pitymys* or *Pedomys*.

Pedomys llanensis Hibbard

(Fig. 8*H*)

Material.—No. 24511, a left jaw with $M_{\bar{1}}$–$M_{\bar{3}}$ but without the incisor, coronoid or angular processes. No. 39604, an incomplete left lower jaw with $M_{\bar{1}}$ and $M_{\bar{2}}$; No. 39605, a fragmentary jaw with $M_{\bar{1}}$–$M_{\bar{2}}$; and isolated teeth. At least 4 individuals are present.

Description.—As in the holotype, the topotype material has fourth and fifth triangles which are confluent with the broad anterior loop in $M_{\bar{1}}$, and confluent third and fourth triangles in $M_{\bar{2}}$ (Fig. 8*H*). The third labial and fourth lingual re-entrants of $M_{\bar{1}}$ are better developed in the topotype material. In No. 39605, there is a shallow, fifth lingual re-entrant containing cement, and a slight fourth labial one without cement. These 2 re-entrants are generally better developed in Recent *Pitymys* and *Pedomys*. The confluence of the third and fourth triangles of $M_{\bar{2}}$ is like that of the holotype. The labial re-entrants of $M_{\bar{1}}$, especially the second, are wide and angular medially. In a study of Recent specimens, I was unable to duplicate the configuration of the re-entrants in 91 specimens of *Pitymys pinetorium* LeConte and 146 of *Pedomys ochrogaster* (Wagner). Typically, the re-entrants of the Recent forms are in the form of anteriorly oriented half crescents. Some individuals of *Pedomys* were observed to have a somewhat angular re-entrant, but they are not as wide medially as in *P. llanensis*. The pit between $M_{\bar{3}}$ and the ascending ramus is deep, but this feature is subject to such extreme geographic variation in Recent *Pedomys* and *Pitymys* that I consider it to be of little diagnostic importance.

Measurements in mm.—Occlusal length of $M_{\bar{1}}$–$M_{\bar{3}}$, 5.9, 1 specimen. Occlusal length of $M_{\bar{1}}$–$M_{\bar{2}}$, 4.5 (4.4–4.6), 3 specimens. Occlusal length of $M_{\bar{1}}$, 2.9 (2.8–3.0), 3 specimens; greatest width of $M_{\bar{1}}$, 1.15 (1.1–1.2), 3 specimens.

Discussion.—The similarity in the nature of the labial re-entrants of *Pitymys meadensis* and *Pedomys llanensis*, and the slight development of the fourth labial and fifth lingual re-entrants in the topotypes of the latter led me to suspect that the two forms might be variants of the same species. A subsequent study of 103 $M_{\bar{1}}$'s and 169 $M_{\bar{2}}$'s convinced me that they are distinct species. I consider No. 24511 to be *P. llanensis* rather than a variant of *Pitymys meadensis* (Hibbard, 1949, p. 74, fig. 2). *Pedomys* or *Pitymys dideltus* Cope from the Port Kennedy Cave deposit of Pennsylvania has an enamel configuration which is similar to *Pedomys llanensis* (Hibbard, 1955, p. 97, fig. 24). However, in *P. dideltus*, the confluence of the third and fourth triangles of $M_{\bar{2}}$ is more constricted and the tooth row is larger (10 per cent) than in *P. llanensis*. Hibbard (1955, p. 91) gave the measurement of 3.8 mm. for an $M_{\bar{1}}$ of *P. dideltus* from the collections of the Academy of Natural Sciences of Philadelphia. This figure is 25 per cent larger than the average for $M_{\bar{1}}$ of *P. llanensis*.

The teeth and lower jaws of Recent North American species of *Pedomys*

and *Pitymys* are so extremely variable that separating criteria do not exist. In a comparative study of *Pitymys pinetorium* and *Pedomys ochrogaster*, I found that 95 per cent of the latter had the fourth and fifth triangles of M_1 confluent with the anterior loop as well as confluent third and fourth triangles on M_2, as compared to 60 per cent in *Pitymys*. This greater frequency, plus the general observation that the labial re-entrant angles of *Pedomys* more closely approach the nature of those of *P. llanensis*, suggest that the Cudahy specimens are *Pedomys*. However, it is not possible to assign this species to either genus with certainty.

Family Zapodidae

Zapus cf. *sandersi* Hibbard

(Fig. 4*A–C*)

Material.—No. 38342, a left jaw fragment with a well-worn M_1; No. 38343, a fragmentary jaw with M_2 and M_3; No. 38344, a lower jaw of an old adult with incisor and M_1; No. 38345, a lower jaw with M_1; No. 38518, an isolated M_1 and M^2. At least 3 individuals present.

Description.—A small *Zapus* with a ramus size near to that of *Z. hudsonius* (Zimmerman). The size, shape, and occlusal pattern of the 4 recovered M_1's are remarkably similar. All are rather blunt and broadly rounded anteriorly. This lends an appearance of stoutness when compared with those of Recent species and is due to the wide protoconid (0.8 mm.). This appearance of bluntness is approached by *Z. hudsonius* only after extremely heavy wear, or in the somewhat exceptional case when a deep anteromedial groove interrupts the protoconid—a feature not present in any known fossil species. No. 38345 (Fig. 4*C*) has a very thin, shallow anteromedial groove similar to that observed in some *Z. trinotatus* Rhoads. This feature is lost early in life. No. 38518 (Fig. 4*B*), which is moderately worn, shows no sign of this groove. The external re-entrant valley of the Cudahy specimens is broad. It is most similar to *Zapus sandersi* Hibbard in this respect. The depth of this re-entrant is more shallow than *Z. trinotatus* and *Z. princeps* Allen. It duplicates the depth observed in *Z. sandersi* and *Z. hudsonius*.

M_2 and M_3 (No. 38343, Fig. 4*A*) are distinct from all specimens of *Zapus* observed. M_2 is subquadrate; that is, wider than the M_2 of Recent species with a similar occlusal length. M_3 is oval in shape and is slightly reduced in size. M_2 and M_3 of *Z. hudsonius acadicus* Dawson most closely resemble these teeth in size, but in *Z. h. acadicus*, M_1 and M_2 are more elongate and slender, and M_3 is larger and generally subtriangular in shape rather than round.

Measurements in mm.—Greatest length of M_1, 1.58 (1.55–1.60); greatest width of M_1, 0.95 (0.9–1.0), 4 specimens each. Occlusal length of M_2, 1.3; greatest width, 0.9, 1 specimen. Greatest length of M_3, 0.8; greatest width, 0.75, 1 specimen. Greatest length of M^2, 1.5; greatest width, 1.15, 1 specimen.

Discussion.—I consider the Cudahy material definitely distinct from any living species of *Zapus*. It may be distinguished from *Z. trinotatus* and *Z. princeps* by its small tooth size and by the shallow depth of its external re-entrant fold in M_1. *Z. hudsonius* is easily separated by its elongate and narrow

tooth row and, in most cases, by the deep anteroconid groove extending well down the anterior face of $M_{\bar{1}}$. *Zapus adamsi* Hibbard is larger and has: (1) a more elongate, narrow tooth row; (2) a deeper external re-entrant fold; (3) a larger $M_{\bar{3}}$ than the Cudahy material. *Z. burti* Hibbard is much larger than the Cudahy specimens and the external re-entrant approach is much shorter in both $M_{\bar{1}}$ and $M_{\bar{2}}$. The nature of this approach is considered to be relatively constant because it does not vary significantly in Recent species. *Z. rinkeri* Hibbard, the largest as well as the oldest known member of the genus, is much too large for consideration.

Z. sandersi of the Aftonian interglacial epoch, is known from a lower jaw fragment with $M_{\bar{1}}$. This tooth is comparable to those of the Cudahy material in both size and shape. The width and depth of the labial and lingual re-entrants are similar, although a slight anterior projection of the entoconid somewhat constricts the external re-entrant of *Z. sandersi*. The approach of this re-entrant is the same in both forms, however. Because these features are relatively constant in Recent species, they are considered significant here.

ORDER EDENTATA

Family Megalonychidae

Megalonyx sp.

(Fig. 4*F*)

A left upper tooth (No. 38403) and a left, second metacarpal of the fourth digit (No. 38404) represent this ground sloth. It was not previously known in the fauna. In cross section, the tooth is elliptical but with a swelling on the lingual side (Hay, 1914, p. 114, Fig. 6). This establishes that it is the anteriormost tooth in the jaw. The anteroposterior length is 34.5 mm., and its greatest width is 15.2 mm. The left metacarpal (Fig. 4 *F*) compares best with the first phalanx of the fourth digit of *Megalonyx*. I am grateful to John J. Stephens for making this comparison with the mounted skeleton of *Megalonyx* at Ohio State University.

ORDER PROBOSCIDEA

Family Elephantidae

Mammuthus sp.

This family is represented by a single plate of a tooth of *Mammuthus*. This is the first record of mammoth in the Cudahy fauna of Meade County.

ORDER LAGOMORPHA

Family Leporidae

Sylvilagus sp.

This is the first record of a rabbit in the fauna. It is represented by a right, upper, cheek tooth; probably M^3. The anteroposterior occlusal length of No. 39573 is 1.95 mm., and the greatest occlusal length is 3.6 mm.

ORDER ARTIODACTYLA

Family Tayassuidae

Platygonus sp.

This peccary is represented by 3 tooth fragments (No. 42345). This is the first record of the genus in the Cudahy fauna.

Family Antilocapridae

Antilocaprid

Two pronghorn teeth (LP_3 and LP_4) which closely correspond to those of *Antilocapra americana* (Ord) were recovered from locality 17. The teeth are well worn and the roots are fully formed. A remnant of an enamel pit is present on P_4; all other pits have been lost with wear. The anteroposterior length of P_3 is 7.3 mm., and that of P_4 is 9.2 mm. The greatest width of P_3 is 5.2 mm. and the greatest width of P_4 is 5.6 mm. This is the first recorded occurrence of the pronghorn in the Cudahy fauna.

ORDER PERISSODACTYLA

Family Equidae

Equus sp.

A horse hoof (No. 38405) and tooth fragments of this genus were recovered. Hibbard (1944) reported 2 molars which compared best with *Equus niobrarensis* Hay. The additional material is too fragmentary for specific identification.

Acknowledgments

I am especially indebted to Claude W. Hibbard for the privilege of studying the Cudahy material and for the numerous, helpful suggestions he has made. Thanks are also due to William H. Burt and Emmet T. Hooper for allowing me free access to the Recent mammal collection in the University of Michigan Museum of Zoology. Robert W. Wilson, Museum of Natural History, University of Kansas, kindly made available to me the holotype material of the Cudahy fauna, and Randolph L. Peterson, Royal Ontario Museum of Zoology, provided me with Recent specimens of *Synaptomys borealis* for comparative purposes. Special appreciation is tendered to John J. Isaacs and LeRoy Marr of Meade, Kansas, and Alfred Shoemaker of North Loup, Nebraska, for permitting fossil collecting on their respective ranches. I also wish to sincerely thank the other members of the field party which collected the material described in this paper. They are: William G. Melton, James Kimbell, John P. Rood, James B. Stevens, and David Winsted.

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LITERATURE CITED

Eardley, A. J., and Vasyl Gvosdetsky. 1959. Pleistocene (Saltair) Core from Great Salt Lake. Geol. Soc. Amer. Bull. (Abstract), 70 (12): 1594–1595.

Franzen, Dorothea S. 1946. A New Fossil Pupillid. Nautilus, 60: 24–25.

——, and A. Byron Leonard. 1947. Fossil and Living Pupillidae (Gastropoda = Pulmonata) in Kansas. Univ. Kans. Sci. Bull., 31 (No. 15, pt. 2): 311–411.

Frye, John C., and A. B. Leonard. 1952. Pleistocene Geology of Kansas. Kans. Geol. Surv. Bull., 99: 1–230, 19 pls., 17 figs.

——, Ada Swineford, and A. Byron Leonard. 1948. Correlation of Pleistocene Deposits of the Central Great Plains with the Glacial Section. Jour. Geol., 56 (6): 501–525, 2 pls., 3 figs.

Gaughran, George R. L. 1954. A Comparative Study of the Osteology and Myology of the Cranial and Cervical Regions of the Shrew, *Blarina brevicauda*, and the Mole, *Scalopus aquaticus*. Univ. Mich. Mus. Zool., Misc. Pub., 80: 1–82, 23 pls.

Getz, Lowell L. 1960. Middle Pleistocene Carnivores from Southwestern Kansas. Jour. Mammal., 41 (3): 361–365.

Hall, E. Raymond, and Keith R. Kelson. 1959. The Mammals of North America. New York, Ronald Press. 1–1162, 553 figs., 500 maps.

Hibbard, Claude W. 1944. Stratigraphy and Vertebrate Paleontology of Pleistocene Deposits of Southwestern Kansas. Geol. Soc. Amer. Bull., 55: 707–754, 3 pls., 20 figs.

——. 1949a. Pleistocene Stratigraphy and Paleontology of Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 7 (4): 63–90, 1 pl., 3 figs. 3 maps.

——. 1949b. Pleistocene Vertebrate Paleontology in North America. Geol. Soc. Amer. Bull., 60: 1417–1428, 2 figs.

——. 1950. Mammals of the Rexroad Formation from Fox Canyon, Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 8 (6): 113–192, 5 pls., 23 figs.

——. 1955. Notes on the Microtine Rodents from the Port Kennedy Cave Deposit. Proc. Acad. Nat. Sci. Phila., 107: 87–97, 2 figs.

——. 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. PMASAL, 41 (1955): 145–200, 2 pls., 16 figs.

Hooper, Emmet T. 1952. A Systematic Review of the Harvest Mice (Genus *Reithrodontomys*) of Latin America. Univ. Mich. Mus. Zool., Misc. Pub., No. 77: 1–255, 9 pls., 24 figs.

Howell, A. Brazier. 1927. Revision of the American Lemming Mice (Genus *Synaptomys*). North Amer. Fauna, No. 50, U. S. Dept. Agri., Wash.: 1–37, 2 pls., 11 figs.

Johnston, C. Stuart, and Donald E. Savage. 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Panhandle of Texas, Part I. Univ. Calif. Publ. Geol. Sci., 31 (2): 27–50, 6 figs., 5 maps.

Leonard, A. Byron. 1946. Three New Pupillids from the Lower Pleistocene of Central and Southwestern Kansas. Nautilus, 60: 20–24.

——. 1948. Five New Yarmouthian Planorbid Snails. Nautilus, 62: 41–47.

——. 1950. A Yarmouthian Molluscan Fauna in the Midcontinent Region of the United States. Univ. Kans. Contrib. Pal., Mollusca, Art. 3: 1–48, 6 pls., 4 figs.

Merriam, C. Hart. 1895. Monographic Revision of the Pocket Gophers, Family Geomyidae (Exclusive of the Species of *Thomomys*). North Amer. Fauna No. 8, U. S. Dept. Agri., Wash: 1–220, 19 pls., 71 figs., 4 maps.

Powers, Howard A., Edward J. Young, and Paul R. Barnett. 1958. Possible Extension into Idaho, Nevada, and Utah of the Pearlette Ash of Meade County, Kansas. Geol. Soc. Amer. Bull. (Abstract), 69 (12): 1631.

Smith, Harold T. U. 1938. Preliminary Notes on Pleistocene Gravels in Southwestern Kansas. Kansas Acad. Sci. Trans., 40: 283–291.

Stephens, John J. 1960. Stratigraphy and Paleontology of a Late Pleistocene Basin, Harper County, Oklahoma. Geol. Soc. Amer. Bull., 71: 1675–1702.

Swineford, Ada. 1949. Source Area of Great Plains Pleistocene Volcanic Ash. Jour. Geol., 57 (3): 307–311, 1 fig.

Tihen, Joe A. 1955. A New Pliocene Species of *Ambystoma*, with Remarks on Other Fossil Ambystomids. Univ. Mich. Mus. Pal., Contrib., 12 (11): 229–244, 1 pl., 1 fig.

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BOTANY

FOSSIL POLLEN ASSOCIATED WITH A LATE-GLACIAL WOODLAND MUSK OX IN MICHIGAN*

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In 1956 Ray Coville of Climax, Michigan, found 3 large vertebrae in a marl spreader loaded with material taken from a marl pit on the Coville Farm, in the southeast corner of the SE ¼ Sec. 18, T. 3 S., R. 9 W., Kalamazoo County, Michigan. He took the vertebrae to Frank Hinds of the Department of Biology, Western Michigan University, for identification. Hinds invited Claude W. Hibbard, the junior author, to collaborate on a study of the vertebrae; and both visited the locality in November, 1956, but no other fossil bones were found. They assigned the bones, an atlas, axis, and third cervical vertebra, to *Symbos cavifrons* (Leidy) and obtained the radiocarbon date of 13,000 ± 600 B. P. in C_{14} years on the third cervical vertebra (Sample No. M-639) from The University of Michigan Memorial-Phoenix Project Laboratory (Hibbard and Hinds, 1960).

The junior author saved the marl matrix removed from the foramen of the atlas, and gave the marl sample to the senior author to examine for fossil pollen. The pollen spectrum shown in Table I resulted from the analysis. Although the pollen spectrum represents the vegetation in the vicinity of the depositing area at only one point in time, the association with remains of a now-extinct large mammal of the Pleistocene and with a radiocarbon date warrants publication of this fragment of postglacial vegetation history.

There is little hope that further samples can be obtained for amplifying the pollen record at this site. Hibbard and Hinds (1960, pp. 103–104) described the deposit as follows:

> The marl pit is situated in a small depression previously occupied by a lake

* Pollen analytical work in this study was supported by a grant from the Horace H. Rackham Fund of The University of Michigan. Alan I. Gebben assisted the senior author in preparation of the material and pollen counting.

TABLE I

FOSSIL POLLEN AND SPORES IN MARL REMOVED FROM MUSK OX (*Symbos*) ATLAS

Found at depth 4 to 6 feet in marl pit on Coville Farm, SE ¼ Sec. 18, T. 3 S., R. 9 W., Kalamazoo County, Michigan

		Number Counted	% ΣAP
TREE POLLEN			
Picea	Spruce	434.5	86.9
Abies	Balsam fir	7	1.4
Pinus	Pine	2.5	0.5
Larix	Larch	5	1.0
Betula	Birch	10	2.0
Carpinus/Ostrya	Blue beech/hop-hornbeam	16	3.2
Juglans cf. *cinerea*	Butternut	2	0.4
Carya	Hickory	3	0.6
Quercus	Oak	16	3.2
Ulmus	Elm	1	0.2
Tilia	Linden (basswood)	1	0.2
Acer	Maple	2	0.4
Total tree pollen (ΣAP)		500.0	100.0
NONTREE POLLEN (AND SPORES)			
Typha latifolia	Broad-leaved cattail	19	3.8
Potamogeton	Pond weed	11	2.2
Gramineae	Grass family	12	2.4
Cyperaceae	Sedge family	12	2.4
Salix	Willow	13	2.6
Alnus	Alder	3	0.6
Chenopodiaceae/Amaranthaceae	Pigweed/amaranth fams.	1	0.2
Caryophyllaceae	Pink family	3	0.6
Ambrosia-type	Ragweed-type	7	1.4
Artemisia cf. *ludoviciana* var. *gnaphalodes*	White sage	12	2.4
Solidago/Bidens-type	Goldenrod/beggars-tick-type	6	1.2
Sphagnum	Peat-moss	3	0.6
Lycopodium	Ground-pine	1	0.2
Polypodiaceae	Fern family	11	2.2
Total nontree pollen (and spores) (ΣNAP)		114	22.8
Unidentified spherical unornamented spores		165	33.0
UNDETERMINED POLLEN AND SPORES		24	4.8

of post-Cary age. The pit was dug in a marshy area. A small stream flowed from the pit into a nearby slough. A layer of muck, ranging from one foot to eighteen inches thick, covered the marl deposit. The depth of the marl varied from six to eight feet. Ray Coville reported that at the time of the removal of the marl which contained the vertebrae, they were operating the power shovel from four to six feet below the water surface. Due to the spring the pit was full of water so that examination of the walls or floor was not possible.

Clean articulation faces on the 3 vertebrae indicated that they had been in attachment in the deposit. It is therefore reasonable to assume that the marl in the foramen of the atlas was intruded shortly after deposition of the bones and is nearly contemporaneous with the bones.

The sediment sample was prepared for pollen analysis by first slowly dissolving the calcium carbonate in 7 per cent (by volume) hydrochloric acid, then by the standard acetolysis treatment. The resulting pollen concentrate was suspended in glycerin jelly, and slide preparations were made from the stock suspension without staining. The preparations are rich in pollen and spores, small fragments of plant cuticles, pieces of very small arthropod skeletons, and silt-size grains of dark minerals. The marl was probably deposited in relatively shallow lake waters.

The pollen spectrum unequivocally records a spruce forest in the vicinity of the depositing area. Relatively low values for nontree pollen indicate that the forest was in a closed stand, not in a parklike stand. The pollen of *Carpinus/Ostrya, Juglans* cf. *cinerea, Carya, Quercus,* and perhaps also *Ulmus, Tilia,* and *Acer* seems out of place with the strongly predominant *Picea.* These hardwood trees, then, may have gained representation here through "long-range drift" pollen or through rebedding of fossil pollen from older deposits. Rebedding of pollen from glacial sediments in late-glacial deposits has been established for a number of localities in recent years (cf. Andersen, 1954, pp. 147–148). If rebedding is invoked as an explanation for this sample, however, the extremely low percentage of *Pinus* pollen is difficult to explain, as *Pinus* pollen occurs widely and in relatively large numbers with these hardwood tree pollens in the North Central States, and it usually survives destructive forces longer than the hardwood pollen grains.

The very strong dominance of *Picea* pollen is encountered only in the oldest layers of deep lake and bog sediment columns in the Lower

Peninsula of Michigan, as in Hidden Lake in Livingston County (Andersen, 1954), Powell Bog in Clare County (Potzger, 1948), and Third Sister Lake in Washtenaw County (Potzger, 1946). This circumstance indicates an early post-last-ice age for the marl layer enclosing the musk ox bones.

In the nontree pollen types *Typha latifolia, Potamogeton,* and possibly Gramineae, Cyperaceae, and *Salix* indicate aquatic vegetation, probably that associated with the pond in which the marl was deposited. The low proportion of *Sphagnum* spores is in agreement with many other early post-last-ice pollen records in the Great Lakes region. *Ambrosia* and *Artemisia* are of interest, as these two genera have been found well represented in the late glacial of Michigan and elsewhere (cf. Andersen, 1954). The *Artemisia* in this sample is almost identical with reference pollen of *A. ludoviciana* var. *gnaphalodes,* a plant of prairies and grassy openings from southern Ontario west to British Columbia and southward (Fernald, 1950, p. 1523). The spores listed as "unidentified spherical unornamented" compare favorably with spores of several genera of mosses, but lack of any distinguishing characters makes even the assignment to mosses uncertain.

The pollen flora of the marl matrix taken from the foramen in the atlas bone indicates that this woodland musk ox lived in an extensive spruce forest that may have contained small proportions of balsam fir, larch, and possibly birch. Local openings in the forest probably occurred on gravelly flood plains and sand plains, where there would have been stands of grasses, with ragweed, sage, goldenrod, other herbs, and willows. Ponds and lakes were occupied by pondweeds and probably by other aquatic plants, and their shores were bordered, in at least some places, by cattails and sedges. The late-glacial landscape in Kalamazoo County had the aspect of the boreal coniferous forest that now exists north of Lake Superior, but the flora did not necessarily include all of the species now associated with the boreal forest. It is also possible that the late-glacial spruce forest in southern Michigan contained floral elements that today belong to communities well south of the boreal forest, especially if those plants were aggressive pioneer species that could have advanced rapidly across the freshly deglaciated areas.

LITERATURE CITED

ANDERSEN, S. T. 1954. A Late-Glacial Pollen Diagram from Southern Michigan, U.S.A. Danmarks Geol. Undersøgelse, Series 2, No. 80, pp. 140–155.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. New York: American Book Co. lxiv + 1632 pp.

HIBBARD, C. W., AND HINDS, FRANK J. 1960. A Radiocarbon Date for a Woodland Musk Ox in Michigan. PMASAL, 45: 103–108.

POTZGER, J. E. 1946. Phytosociology of the Primeval Forest in Central-Northern Wisconsin and Upper Michigan, and a Brief Post-glacial History of the Lake Forest Formation. Ecol. Mon., 16: 211–250.

——. 1948. A Pollen Study in the Tension Zone of Lower Michigan. Butler Univ. Bot. Studies, 8: 161–177.

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AN ANALYSIS OF STREPTOMYCETE POPULATIONS IN SOILS[1, 2]

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Introduction

Streptomycetes are known to abound in most soils, but there is little information on the nature of the populations. Any substantial progress in this area must await fundamental advances in taxonomy and ecology. Valid criteria for the delineation of species have not as yet been agreed upon by taxonomists of actinomycetes although significant contributions have been made (Waksman, 1957, Pridham et al., 1958, Gause, 1958, and Krasil'nikov, 1960). The present work attempts to derive some conception of the populations through an analysis of herbarium specimens of colonies of fresh isolates, a technique which permits survey of massive collections (Jones, 1950). A preliminary report was given in 1956 (Jones, 1956).

Methods

Four soil samples were obtained from each of the following locations: Ann Arbor, Michigan, soils A, B, C, and D; Cheboygan, Michigan (200 miles north of Ann Arbor), soils E, F, G, and H; Eugene, Oregon, soils I, J, K, and L; and Tallahassee, Florida, soils M, N, O, and P. Soils from the first two locations were sampled and studied in the summer of 1952 and the second in 1956. All of the samples were taken from actinomycete-rich sods to give general uniformity of plant cover.

A 50-gram portion of a soil sample was suspended in 500 ml. of sterile tap water and a dilution series prepared. One ml. of the 1:100,000 dilution in soft agar was spread over a basal layer of Jensen's (1930) medium in each of 50 Petri dishes. The plates were incubated for 3 weeks at 28° C. Then all sporulating colonies, from whatever number of plates gave a sum nearest 100, were picked and

[1] Paper No. 1096 from the Department of Botany of The University of Michigan.

[2] Aided by Grant No. 703 from the Horace H. Rackham School of Graduate Studies of The University of Michigan.

transferred to Bennett's (for formula see Jones, 1949) agar slants. From abundantly sporulating slants, transfers were made to five synthetic test media in Petri dishes. Five inoculations were made per plate from a heavy inoculum of spores.

The growths (Fig. 1) were colonies in the true sense, as each arose from a mass of spores. Erikson (1948), for example, found 348 million viable spores per loopful of inoculum from a densely sporulating growth of Streptomyces. She indicated that, "Such mass transfers of typical growth usually yielded uniform growth on plates."

The media used in the 1952 studies of the two Michigan localities were: Krainsky's glucose-asparagin agar; Waksman's (1919) starch agar; Czapek's sucrose-nitrate agar; Jensen's (1930) sodium-caseinate agar and tyrosin agar (Waksman, 1950). In the 1956 studies, glycerol-nitrate, a modification of Czapek's medium, of substituting glycerol for sucrose, was employed in place of tyrosin, which proved a very poor medium for development of either substratal mycelium or spores.

After a 3-week incubation at 28° C. the plates were prepared for use as permanent herbarium specimens (Jones, 1950). In this process, Petri dish cultures were submerged in 1 per cent aqueous mercuric chloride solution to sterilize the agar and to permit its removal as intact discs, which were then dried, mounted, and labeled (Fig. 1). Linear arrangement of the 5 specimens of each isolate on a narrow sheet permitted ready comparison. The dried mounts retained the characteristics of the living cultures remarkably well even to microscopic details of spores and sporophores.

Incidentally the herbarium specimens must be stored in humid atmosphere to prevent the dry agar films from becoming brittle and friable. Specimens thus stored were in excellent condition after six years. The herbarium material has the obvious advantage of being the permanent, bona fide specimens of organisms as first isolated from nature. Apparently mercuric chloride causes the agar films to disintegrate. R. E. Holttum of Kew Gardens informs me that it has the same action on herbarium paper.

Results

The validity of the method used to analyze the populations rests on the likelihood that a fresh isolate will produce similar colonies on a given medium if grown from mass inocula under standard condi-

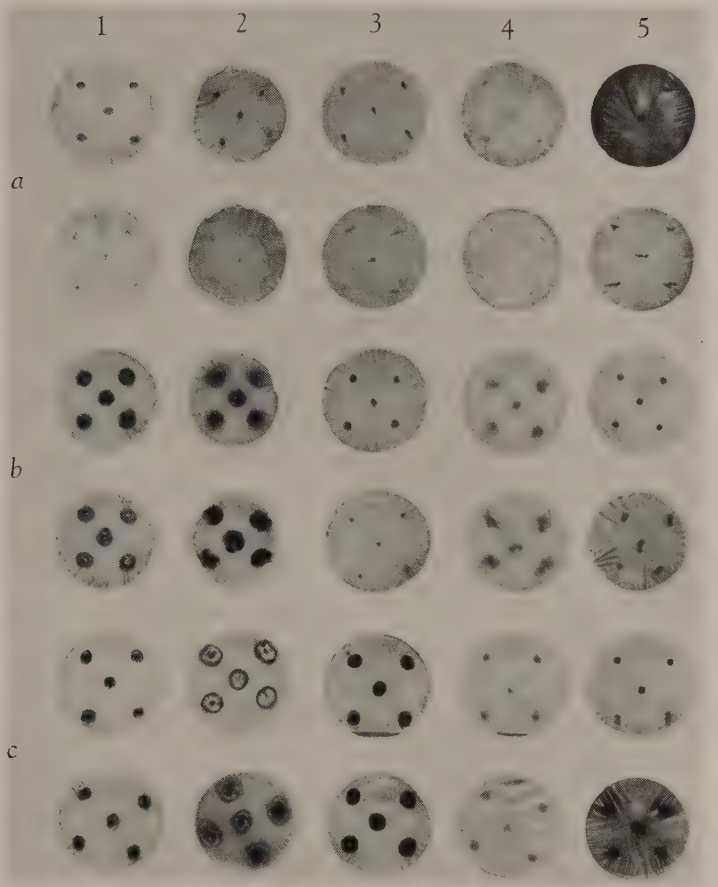

FIG. 1. Six herbarium sheets, each of a different isolate of dried mounts from Petri dish cultures to show the growth patterns of the subgroups: subgroup *a*, the two top rows running horizontally; *b*, the two middle rows, and *c*, the two lowermost rows. The five media are arranged vertically in the following order: 1, Krainsky's glucose-asparagin; 2, Waksman's starch agar; 3, Czapek's sucrose-sodium nitrate; 4, Jensen's sodium caseinate; and 5, tyrosin agar.

tions. To test this, 93 isolates from soil A were grown in duplicate on 5 synthetic media. Eighty-eight or 94 per cent produced similar colonies on each of the media. The most variable isolate, A-87, was replicated 50 times on each medium. Its variability proved to be confined to 1 medium, Jensen's, where 24 per cent produced spores abundantly whereas 76 per cent were asporous and consequently quite unlike in appearance. Considering the well-known variability of actinomycetes, the author considers the method satisfactory though not ideal for a reconnaissance of streptomycete populations.

Fig. 2 gives an arrangement of all the isolates into major groups based on a combination of three characters: the color of the substratal mycelium, growth pattern, and spore color, en masse. In Tables I and II the isolates are distributed into lower taxa, designated in descending order as subgroups and categories purely for convenience without reference to such formal rankings as species or varieties. There are a total of 65 categories of lowest rank. The isolates from one soil sample include 11–21 categories and those of a given geographic region 29–37. Two of the categories occurred in every soil and 9 in every region tested.

The following is an outline of the classification employed:

Group I. Substratal mycelium colorless, buff, yellow, tan, orange to brown
  Subgroup A. Colonies on all media less than 5 mm. in diameter (Fig. 1*a*)
    Category 1. Aerial mycelium absent or if present colorless
    2. Gray-spored (as seen en masse macroscopically)
    3. Black-spored
    4. Blue- or green-spored
  Subgroup B. Colonies 15–25 mm. in diameter on starch agar but less than 5 mm. on Czapek's (Fig. 1*b*)
    Categories 1, 2, 3, and 4 as above
  Subgroup C. Colonies 10–25 mm. in diameter on both starch agar and Czapek's
    Categories 1, 2, 3, and 4 as above (Fig. 1*c*)
Group II. Substratal mycelium black
  Subgroups A, B, and C as above
    Categories 1, 2, 3, and 4 as above
Group III. Substratal mycelium red
  Subgroups A, B, and C as above
    Categories 1, 2, 3, and 4 as above
Group IV. Miscellaneous
    Combinations of characters other than the foregoing. For example, the colors are not in the range enumerated and the growth patterns fall into different arrangements, such as failure to grow on starch.
  Categories 1–36

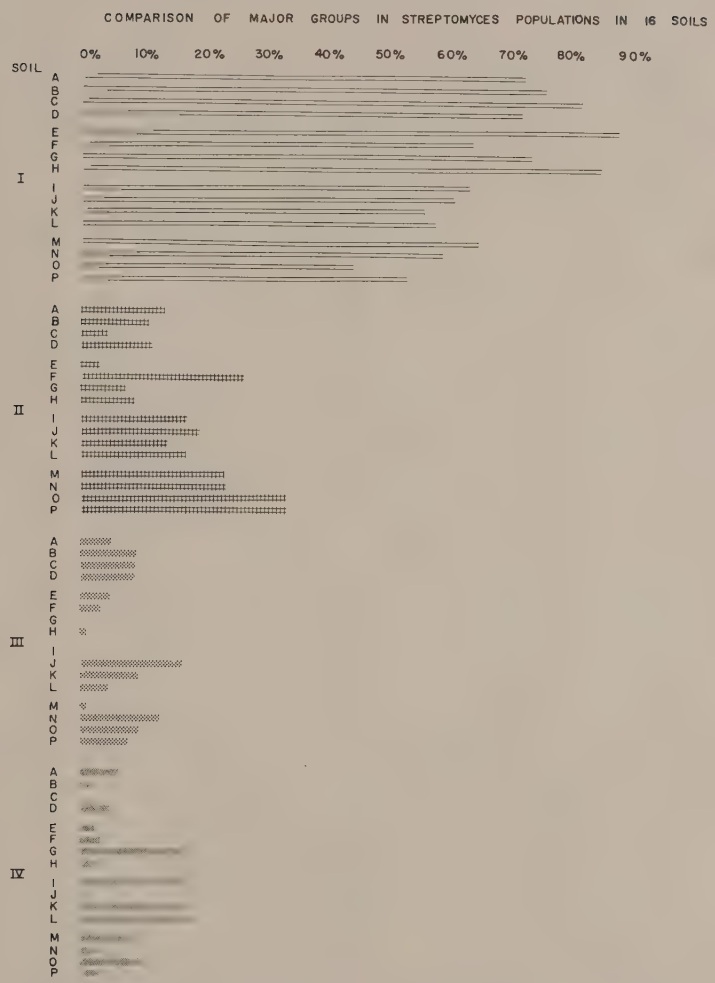

FIG. 2. A comparison of the major groups in streptomycete populations in 16 soils, primarily on the basis of color of the substratal mycelium and spores as viewed macroscopically. The four major groups are designated: I, II, III, and IV. Soils A–D are from Ann Arbor, Michigan; E–H, Cheboygan, Michigan; I–L, Eugene, Oregon; and M–T, Tallahassee, Florida.

TABLE I

AN ANALYSIS OF STREPTOMYCETE POPULATIONS IN SOILS

Streptomyces		Ann Arbor Soils A–D				Cheboygan Soils E–H			
Major groups	Subgroups	A	B	C	D	E	F	G	H
I	A 1	16.1%	16.5%	13.9%	16.2%	8.5%	15.5%	9.8%	9.2%
	2	2.2	4.8	4.6	2.0	3.6	8.3	2.2	0
	3	1.1	5.8	12.8	5.1	1.2	7.1	0	0
	4	0	1.9	0	0	0	0	0	0
	B 1	1.1	1.0	1.2	0	4.9	6.0	2.2	20.7
	2	12.9	2.9	4.6	7.1	9.8	6.0	17.4	39.1
	3	7.5	0	3.5	1.0	2.4	2.4	2.2	1.1
	4	0	4.8	0	0	0	0	0	0
	C 1	3.2	0	1.2	4.0	2.4	3.6	4.3	13.8
	2	16.1	31.0	30.2	23.2	56.1	15.5	29.3	2.3
	3	4.3	1.9	3.5	0	0	1.2	7.6	0
	4	9.7	5.8	10.4	15.2	0	0	0	0
II	A 1	0	1.9	2.3	1.0	1.2	2.4	0	0
	2	0	0	1.2	1.0	0	9.5	0	0
	B 1	0	0	0	0	0	0	0	0
	2	1.1	0	0	0	0	2.4	0	6.9
	3	0	0	0	0	0	8.3	0	0
	C 1	6.4	6.8	0	4.0	0	0	2.2	0
	2	3.2	1.9	1.2	5.1	2.4	2.4	5.4	0
	3	3.2	1.0	0	1.0	0	2.4	0	2.3
	4	0	0	0	0	0	0	0	0
III	A 2	0	1.0	0	0	0	0	0	0
	B 1	0	0	0	0	0	0	0	0
	2	2.2	0	2.3	2.0	1.2	0	0	0
	3	0	0	0	0	0	1.2	0	0
	4	0	0	0	0	0	1.2	0	1.1
	C 1	0	1.0	1.2	3.0	1.2	0	0	0
	2	3.3	7.8	5.8	4.0	2.4	1.2	0	0
	3	0	0	0	0	0	0	0	0
IV	1	2.2			1.0		1.2	1.1	
	2								2.3
	3	2.2							
	4	1.1	1.9						
	5				2.0				
	6						1.2		
	7					2.4			
	8							1.1	
	9								

TABLE I—*Continued*

Streptomyces		Ann Arbor Soils A–D				Cheboygan Soils E–H			
Major groups	Subgroups	A	B	C	D	E	F	G	H
	10								
	11								
	12								
	13								
	14								
	15								
	16								
	17								
	18								
	19								
	20								
	21								
	22								
	23				1.0%				
	24				1.0				
	25								1.1%
	26								
	27							15.2%	
	28								
	29								
	30						1.2%		
	31								
	32								
	33	1.1%							
	34								
	35								
	36								

Group I, which is by far the most inclusive and largest in number of isolates in all soils, has colorless to dark brown substratal mycelium, with various shades between, such as buff, cream, yellow, tan, orange, olive, and light brown. In Group II the substratal mycelium is jet black and in Group III it is red of various shades and hues. The pigment of the substratal mycelium may or may not diffuse into the surrounding agar.

The major groups I, II, and III are each subdivided on the basis of size of colonies into subgroups A, B, and C. Subgroup A (Fig. 1*a*) consists of isolates that grow poorly on all media, with colonies not ex-

TABLE II

AN ANALYSIS OF STREPTOMYCETE POPULATIONS IN SOILS

Streptomyces		Eugene, Oregon, Soils I–L				Tallahassee, Florida, Soils M–P			
Major groups	Subgroups	I	J	K	L	M	N	O	P
I	A 1	5.0%	8.0%	6.9%	11.8%	5.8%	0%	10.4%	15.6%
	2	7.9	0	2.0	7.4	5.8	5.3	3.1	5.6
	3	0	0	2.9	0	0	0	0	3.3
	4	4.0	5.0	0	0	0	0	0	0
	B 1	2.0	0	7.8	0	0	0	0	0
	2	8.9	22.0	13.7	13.2	31.0	26.6	14.6	8.9
	3	0	0	2.9	2.9	1.0	1.1	1.0	1.1
	4	0	13.0	0	0	0	0	1.0	0
	C 1	0	5.0	0	0	4.8	0	0	1.1
	2	30.7	4.0	13.7	19.1	17.5	26.6	14.6	12.2
	3	5.0	0	0	0	0	0	0	0
	4	1.0	5.0	6.9	4.4	0	0	1.0	6.7
II	A 1	2.0	3.0	0	0	5.8	0	0	3.3
	2	2.0	0	0	0	0	0	0	0
	B 1	1.0	3.0	0	0	0	0	0	10.0
	2	3.0	5.0	5.9	0	9.7	10.6	22.9	4.4
	3	0	0	0	0	0	0	0	0
	C 1	0	0	1.0	7.4	0	0	0	0
	2	10.0	6.0	7.8	10.3	8.7	13.8	11.4	15.6
	3	0	3.0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	1.1
III	A 2	0	0	0	0	0	0	0	0
	B 1	0	17.0	7.8	0	0	0	3.1	0
	2	0	0	0	0	1.0	11.7	0	0
	3	0	0	2.0	0	0	0	2.1	0
	4	0	0	0	0	0	0	0	0
	C 1	0	0	0	4.4	0	0	0	0
	2	0	0	0	0	0	0	0	7.8
	3	0	0	0	0	0	1.1	4.2	0
IV	1								
	2								
	3								
	4								
	5								
	6								
	7								
	8								
	9			2.0		1.9	1.1		

TABLE II—*Continued*

Streptomyces		Eugene, Oregon, Soils I–L				Tallahassee, Florida, Soils M–P			
Major groups	Subgroups	I	J	K	L	M	N	O	P
	10			3.9%		1.0%			
	11			2.0				1.0%	
	12				10.3%				
	13					1.0			
	14			8.8	1.5				
	15	1.0%						2.1	
	16				1.5				
	17							5.2	
	18							1.0	
	19	1.0			1.5				
	20						1.1%		
	21					2.9			
	22	6.9							
	23								
	24								
	25								
	26			1.0					
	27								
	28						1.1		
	29					1.9			
	30	8.9							1.1%
	31								1.1
	32								1.1
	33								
	34			1.0					
	35				4.4				
	36		1.0%					1.0	

ceeding 5 mm. in diameter. These are feeble organisms, usually asporous, and lacking strong pigmentation of any kind. They are apt not to survive subculture. Examination of Tables I and II shows that this subgroup comprises 5–42 per cent of the isolates from a given soil sample, which indicates that a large number find the artificial conditions of laboratory culture rather unfavorable. Undoubtedly many members of the natural soil population fail entirely to develop under laboratory conditions and to that unknown extent the actual soil population is not represented in the studies.

Subgroup B (Fig. 1*b*) is characterized by large colonies on Krainsky's and starch agar, but by very poor growth on Czapek's medium. The growth is particularly lush on starch with colonies often 15–25 mm. in diameter. Colonies on the other media seldom exceed 10 mm. in diameter. Starch, incidentally, is the medium of choice for development of streptomycete colonies; for maximum growth of substratal mycelium, sporulation, and pigment production.

Subgroup C (Fig. 1*c*) is characterized by an abundant growth on both starch and Czapek's medium—oftentimes the colonies are of equal size on the two, but those on Czapek's are apt to be thicker and more highly colored, with the pigments soluble. These are choice isolates for laboratory studies.

The subgroups A, B, and C are further divided into four categories on the basis of spore coloration as viewed macroscopically: category 1 may or may not possess spores, if present they are white in color; 2 is gray-spored; 3, black-spored, and 4, green- or blue-spored or a mixture of the two. Unfortunately, class 4 is not clearly defined as its spores may appear gray if viewed under diffuse light.

Group IV is a miscellany of highly divergent isolates of uncommon occurrence. Here one finds unusual pigmentation in the substratal mycelium such as grass green, violet, or golden; growth patterns unlike those ordinarily encountered such as a failure to develop on starch medium only and a wide range of spore coloration on the five media. Of the 36 categories, 26 were each restricted to one soil sample, and 17 were represented by only a single isolate. The Eugene, Oregon, soils yielded a relatively high percentage of isolates from Group IV.

It is significant that the widely divergent isolates often retained a character distinctive to the other isolates of a given soil. For example, practically all isolates from soil N of Tallahassee, Florida, produced a pigment on starch agar which turned yellow in diffuse light but dark brown to black in direct sunlight. All isolates of soil F from Cheboygan, Michigan, developed cartilaginous, fissured colonies on Czapek's medium.

A streptomycete population in every soil examined is a unified aggregate of organisms rather than a miscellany of disjunct taxa. The total range of variation within a population is considerable but the intergradations between isolates are so fine that one is impressed by

the total unity of the population and the difficulty of breaking it into discrete entities.

In every soil, the largest sector of the population can be more or less relegated to the same major group, and in fact its category, IC_2, often predominates over any of the other possible 71 of the same rank.

Whereas I stress that the populations in all soils tested were in general quite similar, I do not mean to give the impression that the isolates of a given region or soil lack uniqueness in the finer distinctions that characterize taxa. Populations as a whole of a given geographic region tend to resemble one another. Some of my observations on these matters are as follows: All of the Ann Arbor soils A, B, C, and D produce clearly similar populations. The Cheboygan soils F, G, and H resemble one another, but E is dissimilar. Populations I, J, and K from Oregon are very similar; L definitely resembles them but for some reason has stronger diffusible pigmentation. The Tallahassee populations O and P are parallel and N shows resemblances to the two; M is an inexplicable oddity.

I believe it likely that as many as two dozen representatives of the approximately 100 composing a population are derived from spores of one mycelium proliferating in the soil sample. I believe that in a large category such as IC_2, the 20 to 40 isolates are derivatives of only 2 or 3 individual organisms. Likewise the few large categories in Group IV are probably each derived from spores of a single mycelium.

Summary

1. This is an attempt to learn something of the characteristics of streptomycete populations in soils.

2. Soil samples from 4 widely separated geographic regions in the United States were collected. Sods were chosen for uniformity of plant cover and proven abundance of actinomycetes.

3. Approximately 100 fresh isolates representing the streptomycete population of each soil were grown as colonies in Petri dishes on 5 synthetic media under standard conditions.

4. The intact agar cultures, after 3 weeks of incubation, were removed from the dishes and dried and mounted as permanent herbarium specimens. The collection consisted of 7,400 cultures of 1,480 fresh isolates on 5 synthetic media.

5. The herbarium mounts retained quite faithfully many properties of the living cultures both macroscopically and microscopically. They have the great advantage of being permanent and always available for study.

6. The specimens were sorted, purely for convenience in analysis, on the basis of color of substratal mycelia, size of colonies on particular media, and spore color en masse.

7. A streptomycete population in every soil examined was a unified aggregate of organisms rather than a miscellany of disjunct taxa. The total range of variation within a population was considerable, but the intergradations between isolates were so fine that one was impressed by the total unity of the population and the difficulty of breaking it into discrete entities.

8. The populations of the four soils, each representing a geographical region, especially tended to be alike. There were many identical or closely comparable isolates occurring throughout the four soils.

9. Few if any isolates of one geographical region closely matched those of another, however similar the general population patterns. Each geographic region clearly imprinted its mark on the characteristics of its organisms, giving them uniqueness.

10. These studies confirm the generally accepted opinion that those interested in the discovery of new kinds of streptomycetes for commercial or purely scientific purposes obtain soil samples from many widely separated geographic regions. On the other hand, one should hope to reisolate several variants of a particular streptomycete from the immediate locale where it was previously obtained.

LITERATURE CITED

Erikson, D. 1948. Differentiation of the Vegetative and Sporogenous Phases of the Actinomycetes. 3. Variation in the *Actinomyces coelicolor* Species-Group. Jour. Gen. Microbiol., 2: 252–259.

Gause, G. F. 1957. Problems in the Classification of Antagonistic Actinomycetes. Moscow. 210 pp. (English translation, 1959, A.I.B.S.)

Jensen, H. L. 1930. Actinomycetes in Danish Soils. Soil Sci., 30: 59–77.

Jones, K. L. 1949. Fresh Isolates of Actinomycetes in Which the Presence of Sporogenous Aerial Mycelia Is a Fluctuating Characteristic. Jour. Bacty., 57: 141–145.

——. 1950. Permanent Mounts of Agar Plates of Streptomyces for Use as Herbarium Specimens. PMASAL, 36: 9–11.

——. 1956. An Analysis of Streptomyces Populations in Soils. Bac. Proc. 1956 Soc. Am. Bac., p. 23.

Krasil'nikov, N. A. 1960. Taxonomic Principles in the Actinomycetes. Jour. Bacty., 79: 65–74.

Pridham, T. G., Hesseltine, C. W., and Benedict, R. G. 1958. A Guide for the Classification of Streptomycetes According to Selected Groups. Applied Microbiol., 6: 52–79.

Waksman, S. A. 1919. Cultural Studies of Species of Actinomyces. Soil Sci., 8: 71–215.

——. 1950. The Actinomycetes. Chronica Botanica Co., Waltham, Massachusetts. 230 pp.

——. 1957. Species Concepts among the Actinomycetes with Special Reference to the Genus Streptomyces. Bacteriol. Revs., 21: 1–29.

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A PECULIAR ISOLATE OF ALLOMYCES[1]

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Allomyces, an aquatic mold with posteriorly uniflagellated swarmers, is best known for the fact that in most species there is an alternation of a diploid, zoospore-bearing plant on which are always borne dark-brown resting spores with thick, pitted walls, and a haploid sexual plant bearing thin-walled gametangia and anisogamous planogametes (Emerson, 1941). Just as the aforementioned resting spores are characteristic of the sporophyte, so the chains of alternating colorless (female) and orange to brick-red-colored (male) gametangia, are marks of the sexual plant.

Recently, a peculiar representative of this genus, of unknown ultimate origin, was isolated from a student's aquarium of tropical fish. Inasmuch as it differs from other known forms in several respects, it seems worthy of note.

Our fungus is highly aberrant in not producing thick-walled pitted resting spores. Even without these, however, it survives long desiccation. Although the isolate's mature reproductive structures are only slightly if at all thicker-walled than the zoosporangia and gametangia of congeneric forms, they would not appear morphologically to be capable of functioning as resting spores. Nonetheless, they have been found to remain viable in dried-up water cultures for at least three months and when immersed in water will produce zoospores.

Another distinctive characteristic is that all fully mature reproructive structures thus far observed are pigmented. No color dimorphism such as found in gametophytes has been detected despite the great variation (Pls. I and II) in shape and size of these bodies. This suggests a possible sporophyte affinity for our plant since at least one species is known, namely *Allomyces moniliformis* Coker and Braxton, 1926, in which the hyphae and sporangia are described as pinkish.

A third peculiarity of this fungus is the strong tendency for its

[1] Contribution No. 1107, Botany Department, University of Michigan.

reproductive structures to be arranged in fully mature plants in *Catenaria*-like fashion, i.e., the individuals occurring in long series and separated by sterile isthmuses (Pl. II *A–I, L*).

The swarmers from all "sporangia" (Pl. I *J*, Pl. II *C, H, J, K*), appear alike in their internal structure, uniflagellate nature, and size, and are of the usual blastocladiaceous type. No fusions or other indications of sexuality have as yet been observed and they appear to function solely as zoospores.

In emphasizing the peculiarity of our isolate we need only point out at this time that it is not known whether we are dealing with a gametophyte or a sporophyte plant.

The morphological features of this fungus upon which we are continuing our investigations are given in the following technical description.

Basal cell variable in size; hyphae sparingly dichotomously as well as sympodially branched, the pseudocells up to 285–315 μ long by 22–27 μ in diameter; rhizoids frequently arising from the elements of the mycelium as well as from the proximal part of the basal cell. Reproductive structures all thin-walled, forming posteriorly uniflagellated swarmers; contents capucine-orange[2]; first-formed ones highly variable in shape especially in clean water cultures, narrowly finger-like and 85–200 μ, 20 μ (Pl. I *B, E*), spherical and 34–40 μ (Pl. I *I–K*), somewhat clavate and 40–55 $\mu \times$ 20–34 μ (Pl. I *C–D, H*), later formed ones usually ovate when terminal, 57–90 $\mu \times$ 35–55 μ (Pl. II *A, C–I, L*), when intercalary 32–80 $\mu \times$ 20–45 μ (Pl. II *B–D, L*), very often in catenulate series and separated from one another by prominent sterile, isodiametric isthmuses 7–60 μ in length; discharge pores 1 to 9, 10–16 μ in diameter, sometimes several on one face only (Pl. I *C–D, H*); swarmers colorless, spherical and 12 μ in diameter, or ovate and 12–16 $\mu \times$ 10–11 μ, with a conspicuous nuclear cap, side body and posterior flagellum (Pl. I *J*, Pl. II *H, J–K*). Resting spores lacking, the structures bearing the swarmers capable of surviving drying. Sexual reproduction not observed.

Isolated on hemp seed from a tropical fish aquarium (legit. F. C. Lundin); ultimate place of origin unknown.

[2] Ridgeway.

LITERATURE CITED

Coker, W. C., and H. H. Braxton. 1926. New Water Molds from the Soil. J. Elisha Mitchell Sci. Soc., 42: 139–147, pls. 10–15.

Emerson, R. 1941. An Experimental Study of the Life Cycles and Taxonomy of *Allomyces*. Lloydia, 4: 77–144, 16 figs.

PLATE I

FIGS. *A–I, K–L. Allomyces sp.* Various types of first-formed reproductive structures. Note long finger-like types as in Figs. *B, E,* and those shown in Figs. *C, D, H,* in which papillae are on one side. Fig. *J.* Spherical reproductive structures discharging swarmers. All figures × 380.

PLATE I

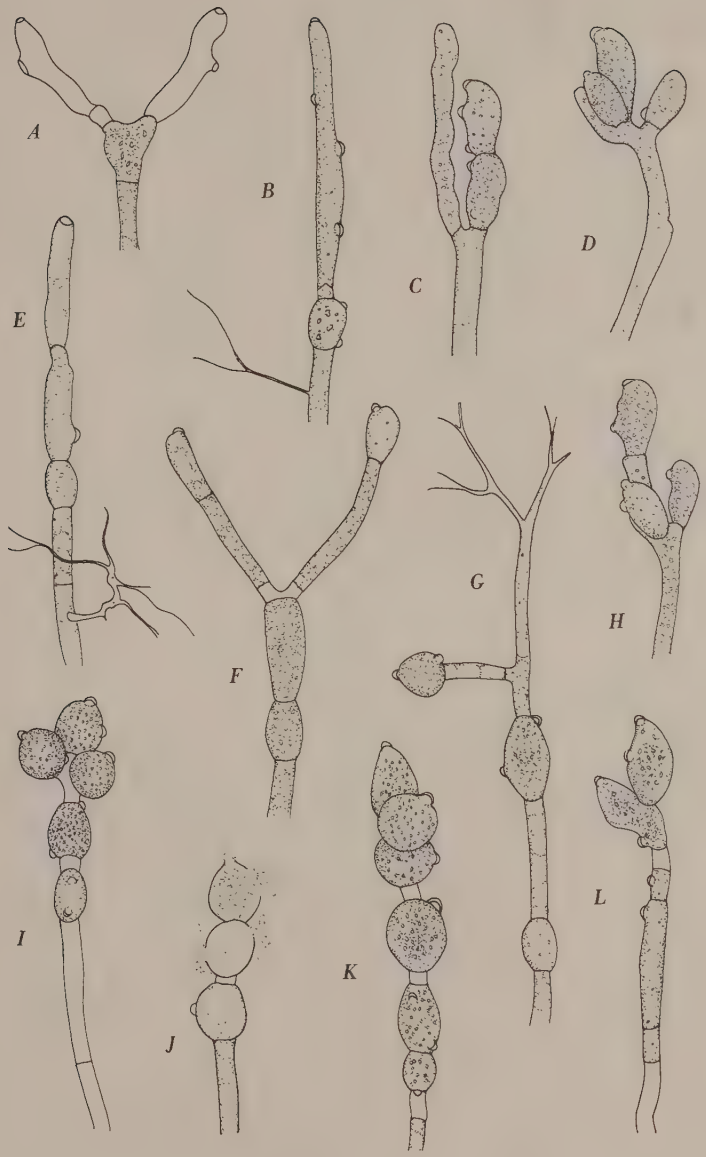

PLATE II

FIGS. *A–I, L. Allomyces sp.* Types of reproductive structures characteristic of fully mature plants. Note in particular the frequent occurrence of sterile isthmuses. Fig. *J*. Terminal reproductive structure discharging swarmers. Fig. *K*. Two swarmers drawn free hand, showing typical internal structure. All figures except $K \times 380$.

PLATE II

Papers of the Michigan Academy of Science, Arts, and Letters
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OBSERVATIONS ON CHYTRIDIACEOUS PARASITES OF PHANEROGAMS

X. NOTES ON SOME SPECIES OF PHYSODERMA OCCURRING IN THE DOUGLAS LAKE REGION OF NORTHERN MICHIGAN

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In the course of an extensive survey of members of the Physodermataceae occurring in the vicinity of the University of Michigan Biological Station at Douglas Lake, species of *Physoderma* have been encountered on a wide variety of hosts. Some of these have already been reported (Sparrow, 1952, 1956, 1957a; Johns, 1958; Sparrow and Johns, 1959). The present paper records the occurrence in the same area of others, at least two of which may be ascribed to already recognized species of earlier authors, two are described as new, and the rest are merely described but not named because certain essential features of their morphology are not as yet known. It is likely that some of the latter may be shown in the future to be distinct species. At the moment, however, the delineation of species of *Physoderma* is a difficult task so that it has seemed best to proceed with caution not only in identifying our fungi with known species but also in establishing new ones.

Physoderma on *Ranunculus acris*

Plants of the Common Buttercup infected with a *Physoderma* appeared in 1959 in a field adjacent to a swale. The latter area had for several years past yielded species of *Physoderma* on various phanerogamic hosts but never on *Ranunculus*. In the 1959 season, water in the swale was unusually high and in

[1] Acknowledgment is made to the National Science Foundation for financial support given this project. It is also a pleasure to acknowledge the considerable assistance of R. M. Johns.

[2] Contribution No. 1104, Botany Department, University of Michigan; contribution from the Biological Station, University of Michigan.

the early spring had flowed into contiguous, low-lying areas of the aforementioned field.

It was obvious, even in mid-June, at which time the water level had receded, that *Physoderma*-infected plants of *Ranunculus* occupied only sites in the field which had earlier been submerged. Not only were these sites still damp but large mats of dried, filamentous algae clung to the plants of *Ranunculus*. The pattern of relationship between earlier submergence and infection was even more clearly discernible when infected plants were marked with stakes and the whole area roughly plotted.

Infected and uninfected plants did not differ from one another save that the former bore on the lower parts of the stem dark brown to black flecks and slightly elevated pustules as well as a few widely separated ones on the leaves.

Identification of the fungus with already described species will not be attempted until more is known of the morphology and spore germination. The resting spores, which are pale amber-colored, ellipsoidal, and slightly flattened on one surface, are 15.6–25 μ × 18.7–31.2 μ, and closely resemble in size those produced by the *Physoderma* found by Karling (1956) on *Ranunculus pusillus* from Louisiana where it was associated with *Synchytrium ranunculi*. On the last-named phanerogam the resting spores were 18–28 μ × 24–32 μ. The resting spores of *Physoderma flammulae* (Büsgen) de Wild. on *R. flammulae* described as 21–32 μ, are not significantly different in size from those of the Michigan material, and the same may be said of those of *P. vagans* Schroeter on various species of *Ranunculus*, which are cited as being 15–30 μ × 20–35 μ. A more complete description than the following one must await the results of further study.

Epibiotic stage not observed. Endobiotic stage bearing ellipsoidal, pale amber-colored, ellipsoidal resting spores, slightly flattened on one surface, wall 2 μ thick, crowded in the subepidermal host cells, those on the stem 18.7–31.2 μ (av. 24.5 μ) × 15.6–25 μ (av. 19.6 μ), those on the stipule 18.7–34.3 μ (av. 24.8 μ) × 15.6–31.2 μ (av. 21.3 μ), germination not observed.

Forming dark brown to black flecks and low pustules on the lower parts of the stem and a few widely separated pustules on the petiole and blade of the leaf of *Ranunculus acris*; Cheboygan County, Michigan.

Physoderma on *Caltha palustris*

Physoderma—infected *Caltha palustris* has been obtained from three different sites in the vicinity of the Biological Station. Admittedly, the proper disposition of this material with respect to the three species of *Physoderma* now described from *Caltha*, namely, *P. calthae* Bucholtz, *P. bohemicum* Sacc., and *P. vagans* Schroeter is difficult. This is due primarily to the fact that these species have been erected as specific entities solely from their resting spore stages, which are little different from one another. Supposed distinctions between them based upon macroscopic appearance of the host reactions are also of little worth since variability even on one leaf of this character is too great to be of significance. Furthermore, color is not a reliable criterion, for it was noted in the infected Michigan material of *Caltha* that young pustules were lead-colored; then, as these matured, they became cinnamon-colored and finally black. Hence, if

color is of value, state of maturity at the time of collection becomes a factor of significance. As to whether the "*Physoderma vagans*" reported on *Caltha* can indeed be assigned to Schroeter's "species" and not to Bucholtz's or Saccardo's, it is impossible to say with the meager information at hand.

Since so little is known of these earlier-described species and, since, obviously, no further elucidation of them from living material by their authors is possible, it seems futile to identify our collections with any of them. The present fully known fungus is, therefore, described as new even though it may encompass some or all of the species based on resting spores found in *Caltha palustris*. The description is based on data from abundant collections made in Hebron Township, Cheboygan County, Michigan, of which both epibiotic[3] and endobiotic stages were studied. It is a pleasure to name this species for R. M. Johns, who has been of such great assistance in furthering the work on *Physoderma*.

Physoderma johnsii sp. nov.

Epibiotic sporangium somewhat irregularly slipper-shaped above, gibbose in side view, lobed, transversely placed; unexpanded portion of the zoospore cyst not often visible, opposite the 10 μ broad discharge papilla; mostly 50 μ long by 10–15 μ to 20–38 μ in diameter; secondary sporangia formed by internal proliferation; rhizoidal system composed of bushy delicate rhizoids, not apophysate; zoospores globose, 5 μ in diameter, with an eccentric refractive, colorless lens-shaped globule and posterior flagellum. Endobiotic system extensive, much branched, delicate, with one, or 2–5-celled turbinate cells, 15–20 $\mu \times$ 3–10 μ; resting spores yellow-ochre, subspherical to oval, sometimes somewhat angular or irregular, with a double apparently unpitted wall 1.5–2 μ thick, 1–3 in a cell, rarely in the epidermal cells, 27.2–38.4 $\mu \times$ 17.6–30.4 μ, germination not observed.

Producing at first lead-colored, later brownish-lilac or cinnamon-colored, eventually black, round to elongate, slightly raised, occasionally acervulus-like pustules 0.5–1 mm. wide on the lamina (primarily lower surface) and petioles of *Caltha palustris* Cheboygan County, Michigan.

Physoderma johnsii n. sp.

Sporangium epibioticum aliquanto inequaliter desuper formata simile soleis, gibbum ab lateribus, lobatum, transversum affixum; partem inexpansam cistellae crassivallatae plerumque non visam, papillae 10 μ latae deliquescenti oppositam; plerumque 50 μ long., 10–15 μ ad 20–38 μ diam.; sporangia secondaria proliferatione interna formata; systema rhizoideum tenuissimum breviter ramosum, non apophysatum; zoosporae sphericae 5 μ diam., cum uno globulo excentrico pellucido, in forma lenticulari et flagello posteriore. Systema endobioticum extense ramosum tenuissimum; cellulis turbinatis 1–5 cellularum 15–20 $\mu \times$ 3–10 μ; sporae perdurantes fulvae colore aliquantulum globosae ad ovatas aliquando angulares vel irregulares, membrana duplice 1.5–2 μ, evidenter absque excavationibus, 27.2–38.4 $\mu \times$ 17.6–30.4 μ in una cellula, germinatione nondum observata.

[3] Gametangial stage.

Producens primum plumbeum colorem, postea purpuram-bruneam vel fulvum, postremo nigrum, globulum ad productum parum sublatum, aliquando apparenter acervulae pustules 0.5–1 mm magnis in laminis praecipue subtus et petioles *Calthae palustris*, in vicinitate "Douglas Lake," Michigan.

Type specimen in University of Michigan Herbarium.
Coll. F. K. Sparrow and R. M. Johns.
Hebron Mud Creek.
Cheboygan Co., Mich.
July 7, 1958.

Physoderma on *Rorippa islandica* var. *hispida*

Plants of *Rorippa* infected with this *Physoderma* have been collected on host plants growing at only one site in the vicinity of the Biological Station. Abundant spore material was obtained for germination and although after collection it was kept damp in a cold room at 5° C. it had all germinated by the time (March) studies on it were initiated. This suggests that the resting spores do not require a period of dormancy and may possibly germinate in the autumn and infect overwintering rosettes of the host.

Epibiotic stage not observed. Endobiotic system extensive, much branched, delicate, with septate turbinate cells; resting spores golden, circular in outline from above and slightly flattened on one surface in side view, 21.87–31.25 μ $\times$ 28.12–34.37 μ (av. 26.75 $\times$ 32.12 μ), wall 2 μ thick, germination not observed, probably opening by a lid.

Forming elongate pustules with rounded ends up to 5 mm. $\times$ 1.5 mm., which are sometimes confluent and up to 100 mm. in length, low, or up to 0.5 mm. high, brown or pale yellow-brown with dark brown centers; primarily on the lower parts of the stem, rarely on the leaves where the pustules are 0.5–1.0 mm. in length. At full maturity the host epidermis fragments freeing the dark brown powdery spore mass. On *Rorippa islandica* var. *hispida*, Emmet County, Michigan.

Karling (1956) has given a brief account of a species of *Physoderma* on the same host collected by W. J. Cody and C. C. Loan in Alberta. It differs from the present material, primarily in the color of the "galls" (lavender-red to reddish brown) produced on the host and in the fact that it is apparently confined to the leaves, a part rarely attacked in our material. The spores of the Canadian fungus are not significantly different in size (16–26 μ $\times$ 28–36 μ). "*Physoderma vagans* Schroeter" has also been listed as occurring on a member of this host genus (*Rorippa amphibia*).

Physoderma comari (Berkeley and White) Lagerheim

This species, which occurs on *Potentilla palustris*, has been recorded from 5 different sites in our region over a period of 3 summers. Resting spore formation is evidently initiated either very early in the growing season or during the previous autumn, for during a search for ephemeral sporangia (Sparrow and

Johns, 1959) the second week in May, 1958, when the leaves of the host were still under a foot of cold water and had not as yet unfolded, nearly mature resting bodies were found.

Inasmuch as further observations are needed on the ephemeral sporangial stage, this phase will not be included in the following description. No data have heretofore been published on the vegetative parts of the endobiotic thallus, and the species has been based solely on a description of the resting spores.

Physoderma comari (Berkeley and White) Lagerheim, emend.

Epibiotic sporangia not known with certainty. Endobiotic thallus composed of a delicate system of rhizoids which ramifies throughout the host tissue and which bears numerous pyriform or ovoid nonseptate or once-septate transversely turbinate cells 9.37–12.5 μ long by 6.25 μ wide, and terminal, pyriform, smaller turbinate structures bearing distal tufts of finger-like haustorial outgrowths; resting spores crowded in the subepidermal cells, hyaline, with a very faintly brown, fragile wall 1–1.5 μ thick, broadly ellipsoidal 22–28.5 $\mu \times$ 23.8–36.5 μ, germination not seen.

Forming on the leaves rounded to more or less elongate separate pustules which are at first whitish later dark reddish-brown to black; when on the leaf lamina tending to cluster on and along the midrib where they are rounded and 0.5 mm. in diameter or elongate and up to 1 mm. in length, on the stipules elongate and up to 2 mm. long by 0.5 mm. wide, and reddish to reddish-brown. Emmet and Cheboygan counties, Michigan.

Whether the fungus ascribed by Schroeter to "*Physoderma vagans*," on *Potentilla anserina* belongs here awaits further study.

Physoderma on *Sium suave*

The occurrence of *Physoderma* on this host has previously been noted in the United States by Davis (1919) in Wisconsin and by Sparrow (1956) in the vicinities of Ann Arbor and Douglas Lake, Michigan. Searches over the past 4 seasons in the last-named region have revealed it at 4 different sites, 3 in Cheboygan County and one in Emmet County. In Northern Michigan in wet years the fungus is abundant, whereas, if there is little precipitation during the winter and spring, as in 1958, and the swampy habitats of the host are relatively dry, few infected plants of the host can be found.

Two sites in the vicinity of the Biological Station were noteworthy for the stands of infected *Sium suave* they supported. The first of these was a swale contiguous with the field containing the *Physoderma*-infected *Ranunculus* earlier described. This same area also had growing in it *Mimulus ringens*, *Lobelia cardinalis*, and *Eleocharis smallii*, all of which were infected with *Physoderma*. No attempt was made in the swale to estimate the percentage of infected *Sium suave* plants, but it was easily seen to be considerable. Such was done, however, for *Sium* plants growing in a roadside ditch in which it was known that water from Douglas Lake had backed up during the spring. On July 10, 1959, a segment of this ditch, approximately 345 feet long by 5 feet wide, by then without standing water and nearly dry, was traversed, and infected and uninfected plants

counted. Of the 180 plants present, 108 or 60 per cent were infected by *Physoderma*. In a very low part of the ditch, still soggy underfoot, of the 43 plants present, 40, or nearly 90 per cent were infected. It was noted that seedlings and plants growing on the higher sides of the ditch were uninfected.

The manifestations of the parasite on the host are probably the most impressive of that caused by any species of *Physoderma* we have encountered. Stems, leaves, and, to a lesser degree, inflorescences are attacked. On the lamina of the leaflets conspicuous separated, target-spot-like black pustules up to 5 mm. in diameter are produced on both surfaces, whereas on the leaf petiole, rachis, and stem, galls up to 1 cm. long by 9 mm. wide by 7 mm. high are formed. In all instances, these pustules and galls are cream-colored at first, later forming a conspicuous reddish-brown central area which at full maturity is brownish- to jet-black and often iridescent. In all types of hypertrophies the epidermis of the host areas is retained intact, frequently until late November. Eventually, it fragments and the ripe spores are dispersed.

A full account of the structure, reproduction, spore germination, and host range of this fungus is in preparation. Most of the essential features of its morphology and reproduction are now known and are included in the diagnosis below.

In describing this species as new, the author has been impelled by several circumstances. Of the various members of the Physodermataceae described on umbelliferous hosts, those which are not, in fact, bona fide species of *Urophlyctis* (*U. pluriannulata, U. hemisphaerica,* etc., are known only from their resting spores. This stage is scarcely distinctive enough in itself, in the author's opinion, to be a trustworthy feature in distinguishing species, even when statistical data on size are included. To be sure, the type of resting spore germination, whether by the circumcissle dehiscence of a cap or by an irregular fracturing of the spore wall, one or other of which is constant in a given species, is likely to be of taxonomic value. No spore germination, however, has been recorded for any true species of *Physoderma* on Umbelliferae. Where it has been followed in *Urophlyctis pluriannulata* on the umbelliferous *Sanicula* (Sparrow, 1957b), an irregular splitting of the spore wall occurred, not a circumcissle one, as here.

Physoderma vagans Schroeter, reported on a species of *Sium*, among other hosts, should be considered. It will be recalled that it was this species to which the present fungus was at first assigned (Sparrow, 1956). As described in the literature, this apparently omnivorous fungus has been said to attack members of the Ranunculaceae, Umbelliferae, and Rosaceae and a diagnosis of it includes the various species of hosts, together with the rather wide size limits of the resting spores, "15–30 × 20–35 μ." No further information is available. *P. vagans* will always be difficult to interpret since its author considered all the resting spore stages found on the various hosts to belong to one fungus but provided no data to substantiate this fact. One is forced to agree with Fischer (1892), who states with respect to *P. vagans*, "Welche Gründe Schroeter bestimmt haben, die auf verschiedenen Familien wachsenden Formen in eine Collectiv-Species zu vereinigen, weiss ich nicht." To be sure certain species of *Synchytrium* have been proven to have very wide host ranges and it is possible that the same may

be shown in the future to be true in some instances in *Physoderma*, but there is no experimental evidence for it now.[4]

It seems justifiable, therefore, rather than to attempt to identify the present morphologically well-known entity with an existing species based solely on the mature resting spores, to describe it as new. Future host-range studies and the like can then be centered around a rather completely known taxon.

Physoderma palustris n. sp.

Epibiotic sporangia gibbose in side view, transversely placed on the underwater dissected leaves of the host, predominantly 15–28 μ long by 12–18 μ high, bearing an apical, 4–5 μ in diameter, thick-walled unexpanded portion of the zoospore cyst; zoospores approximately 20, spherical, 4–5 μ in diameter, with an eccentric colorless globule, small lateral granule, conspicuous nuclear cap and posterior flagellum, escaping through a pore formed upon the deliquescence of a prominent terminal discharge papilla; internally proliferous; rhizoidal system delicate, bushy. Endobiotic stage composed of an extensive, delicate, much-branched rhizoidal system bearing numerous usually once-septate turbinate cells 7–10 $\times$ 12–15 μ; resting spores crowded in subepidermal cells, somewhat ellipsoidal, with one surface slightly flattened, pale amber-colored 18–30 μ $\times$ 17–29 μ (av. 24.6 μ $\times$ 20.8 μ), with a 2 μ thick wall, upon germination producing a broadly conical sporangium 28 μ long which protrudes from the resting spore after the dehiscence of a lid 20 μ in diameter on the flattened surface; zoospores somewhat ovoid, 5–6 μ $\times$ 3–4 μ, with a colorless eccentric globule.

Forming black target-spot-like pustules up to 5 mm. in diameter on the leaflets, and brownish to jet black often iridescent galls up to 1 cm. long by 9 mm. wide by 7 mm. high on the stem, petioles, and rachis of leaves of *Sium suave*; Washtenaw, Cheboygan, and Emmet counties, Michigan; Wisconsin, Davis (1919).

Physoderma palustris sp. nov.

Sporangium epibioticum gibba ob lateribus, transversum affixum in foliis dissectis submersis, plerumque 15–28 μ longis $\times$ 12–18 μ altis, apico 4–5 μ diam. parte inexpansa cistellae crassivallatae praeditum; zoosporae circa 20, globulae, 4–5 μ diam. cum globulo hyalino eccentrico et granula parva laterale, cupula nucleari conspicua et flagello positico praeditae, liberatae deliquescentia papillae singulae conspicuae terminalis. Sporangia secondaria proliferatione interna formata. Systema rhizoideum tenuissimum breviter ramosum. Systema endobioticum extense ramosum tenuissimum; cellulis numerosis turbinatis plerumque uniseptatis, 7–10 μ $\times$ 12–15 μ; sporis perdurantibus numerosis in cellulis subepidermalibus, ellipsoideis unilateraliter applanatis, luteis, 18–30 μ $\times$ 17–29 μ (av. 24.6 $\times$ 20.8 μ), membrana crassa 2 μ, germinatione ab operculo 20 μ diam. in latere applanato dehiscentibus. Sporangium late conicum 28 μ longis; zoosporis ovoideis, 5–6 μ $\times$ 3–4 μ, globulo excentrico pellucido.

[4] In preliminary work on the host range of the Sium parasite it could not be induced to infect *Potentilla anserina, Ranunculus flabellaris, Rorippa islandica,* or *Sanicula gregaria*. Further work is, however, needed to confirm this.

Nigras pustules, puncta, ad 5 mm. diam. in foliis, et intumescentia brunea ad nigra formans, saepe iridescentia, ad 1 cm. longis × 9 mm. latis × 7 mm. altis in caulibus, petioles et rachis foliorum Sii suavis: Washtenaw, Cheboygan et Emmet counties, Michigan; Wisconsin, Davis (1919).

Type specimen in University of Michigan Herbarium.
Coll. F. K. Sparrow and L. E. Wehmeyer.
Ditch by Ypsilanti Airport on U.S. Route 23.
Washtenaw Co., Mich.
July 8, 1937.

Physoderma on *Asclepias incarnata*

The *Asclepias* parasite has been found thus far at only one site in the region although it is undoubtedly more widespread. As in certain other species, the thallus seemed confined to the cortex region of the stem. No *Physoderma* has heretofore been reported on a member of the Asclepiadaceae. That the present fungus has not been described before is surprising in view of the conspicuous markings produced by it on the host stem.

Epibiotic stage somewhat slipper-shaped, gibbose with an apical unexpanded portion of the zoospore cyst, mostly 27–29 μ long by 9–14 μ high by 14 μ at greatest width; zoospores in some sporangia with an orange-colored eccentric globule, in others with a colorless one, fusiform, 5–7 μ long by 3 μ wide, escaping by a terminal pore 7 μ in diameter; rhizoidal system bushy. Endobiotic system delicate, much branched with nonseptate or once-septate turbinate cells 9.37–12.5 μ × 6.25 μ; resting spores one to several in a host cell, pale amber-colored with a wall 1.5–2 μ thick, 15.6–25 μ × 21.8–28 μ (av. 21.75 × 25.5 μ) germination by the dehiscence of a lid, zoospores 3 × 5 μ.

Producing on the stem dark red elongate spots and streaks, sometimes a darkening and rumpling of the epidermis and rarely, on lowermost part, large separate or confluent flattened galls up to 2 cm. wide by 1 cm. high on *Asclepias incarnata*, Emmet County, Michigan.

Physoderma menthae Schroeter

Schroeter's species, which in our area has been collected at four different sites over a period of three years, has been heretofore known only from the resting spore stage. The following expanded account, based upon the Michigan material, includes a description of the epibiotic stage recently published by Sparrow and Johns (1959). From Schroeter's account no significant differences in the size, shape, and color of the resting spores are apparent between the European and American material.

Physoderma menthae Schroeter, emend.

Epibiotic "sporangia"[5] on the glandular trichomes of the stem, pyriform or

[5] Probably gametangia.

somewhat anatropous, transversely placed, 40–52 μ long, the narrower end 6–8 μ, the broader, 18–25 μ in diameter, with a thick-walled, beaklike apex 6–8 μ in diameter, the whole attached near the narrower end to a short, bushy, endobiotic system of delicate rhizoids that arises from an inconspicuous apophysis; fully mature zoospores (gametes ?) not seen; discharge pore 5–7 μ in diameter, at the broad end of the sporangium; internally proliferous. Endobiotic system extensive, much branched, delicate, with once- or twice-septate turbinate cells; resting spores golden, ellipsoidal flattened slightly on one surface, wall 2 μ thick, pitted, 21.7–34.37 × 18.7–31.2 μ (av. 25.3 × 29.6 μ) dehiscing by a lid upon germination and forming a finger-like thin-walled sporangium, zoospores not observed.

Producing broadly to narrowly ellipsoidal pustules up to 2 mm. long by 1–1.5 mm. wide and up to 1.0 mm. in height; usually confined to the internodes of the stem, occasionally forming rounded pustules 0.5 mm. in diameter on the leaves. Pustules whitish at first turning cinnamon-colored and finally black with age. Old pustules powdery, leaving a cavity in the host part after the spores are shed.

Parasitic on *Mentha arvensis* var. *villosa*, Cheboygan County, Michigan.

Physoderma on *Mimulus ringens*

Like some of the preceding species this fungus has been observed over a period of four years and at four different sites in the vicinity of the Biological Station.

Several species of the Physodermataceae have been described on members of the Scrophulariaceae, to which family *Mimulus* belongs. *Urophlyctis linaricola* Spegazzini, as Karling (1950) points out, hardly merits consideration, bearing as it is said to do solitary resting spores 75–150 μ in diameter. Under the binomial *Physoderma negeri* Karling, that author places several physodermataceous fungi on *Euphrasia officinalis* and *Odontites rubra*, the resting spores of which are 38–40 μ in diameter. The question of the identity of the several fungi placed under Karling's binomial will not be discussed but will be left for a later paper.

A description of the Michigan material on *Mimulus* is given below.

Epibiotic stage not observed. Endobiotic system extensive, much branched, delicate, bearing once or several times septate turbinate cells 10–18 × 7–8 μ; resting spores ellipsoidal, flattened on one surface, when young bearing a few supraequatorial, once-branched, antler-like haustorial processes, mature spores crowded in host cells, pale amber with a darker 2 μ thick wall, 16.5–27 μ × 13.5–25.5 μ, upon germination dehiscing a lid and forming a thin-walled, finger-like sporangium within which ellipsoidal, 5 × 3 μ zoospores are produced.

Forming streaks or scarcely raised cinnamon-colored pustules 1.5–2 mm. long by 0.5 mm. wide usually on the lower internodes of the stem, separate or aggregated in great numbers; occasionally forming rounded pustules 0.5 mm. in diameter on the leaves of *Mimulus ringens*; Cheboygan County, Michigan.

Physoderma on *Lobelia cardinalis*

Four sites in the vicinity of the Biological Station have been found in 1958–59 to harbor stands of *Lobelia cardinalis* infected by a species of *Physoderma*.

Infected plants are readily recognizable by the conspicuous markings described below.

Epibiotic stage not observed. Endobiotic system extensive, composed of delicate branched rhizoids and once or several times septate turbinate cells 9.37–15.6 $\mu \times$ 4–6.25 μ; resting spores pale amber-colored, circular or ellipsoidal in outline, and slightly flattened on one surface, 18.75–28 $\mu \times$ 25–31.2 μ, average 22.87 $\times$ 28.00 μ, germination not observed.

Producing ellipsoidal pale, scarcely raised, red-margined spots up to 1 cm. long by 2 mm. wide; scattered, in lines, or covering entire lengths (up to 15 cm.) of the stem, primarily the lower parts; occasionally extending into the base of the leaf along the midrib; rarely producing dark red, 1 mm. in diameter spots on the lamina; on *Lobelia cardinalis*, Cheboygan County, Michigan.

Discussion

Several aspects of the present study seem worthy of further comment and elucidation.

Field studies have made it quite obvious that in our area, at least, there is a very definite relationship between submergence of the host plant early in the growing season and its infection by *Physoderma*. A particularly clear instance of this was afforded by the observations on plants of *Ranunculus acris* growing in the field contiguous with a swale. Here, the pattern of infected and uninfected plants was directly related to whether or not standing water had been present earlier in the season. Those in low-lying, damp ground, covered with dried algae were uniformly infected, whereas those on higher ground were not. Other instances of the association of standing water and infected host plants might be cited. For example, the distribution of infected plants of *Sium suave* in the roadside ditch, mentioned in connection with *Physoderma palustris*, and the direct relationship observed there between number of plants infected and the dampness (hence, lowness) of the ground. The reason for this is explained by Sparrow and Johns' (1959) findings with respect to the occurrence in nature of the epibiotic, presumably gametangial plant. This delicate stage which gives rise to free-swimming structures (probably gametes) has been found by them early in the spring during periods of high water when the host plants are submerged. At this time gametes are readily discharged, probably fuse to form zygotes and accomplish infection of the host plant while it is still under water. Once inside the host, free water is no longer necessary, and the parasite can complete its development under the drier conditions prevailing later in the season. Inasmuch as free water is also necessary for the germination of

the resting spores, by which process the structures giving rise to the epibiotic phase are formed,[6] it can be readily seen how very important early spring high water is to the propagation of the parasite. It is not surprising therefore, that, after a winter and spring of comparative drought, little *Physoderma*-infected material is found, whereas after a winter and spring of heavy precipitation infected plants are abundant.

A puzzling and challenging problem is posed by the swale so frequently mentioned. In this area, which is cut across by a road into east and west portions, no fewer than nine different host plants are known to be infected by *Physoderma*. The question arises as to whether we are dealing here with a single omnivorous species, with several, or with nine distinct ones. Indeed, rather than an omnivorous species it is possible that we have in this swale several or perhaps many distinct species which, because of optimum conditions for infection and growth, have developed side by side. It could also be that some of these have restricted, others unrestricted host ranges. A series of cross-inoculation studies would presumably give us the answer. Unfortunately, however, such is not easy, for at the moment successful germination of *Physoderma* resting spores, the starting point of such studies, is a highly unpredictable business.

Finally, it is peculiar that no genuine species of *Urophlyctis* have been found. This may be attributable to the fact that primarily aquatic and swampy sites have thus far been investigated whereas species of this genus seem to be found most often on more strictly terrestrial hosts.

LITERATURE CITED

Davis, J. J. 1919. Notes on Parasitic Fungi in Wisconsin, VI. Trans. Wisconsin Acad. Sci. Arts and Letters, 19: 705–715.

Fischer, A. 1892. Die Pilze Deutschlands, Oesterreichs und der Schweiz. Rabenhorst, Kryptugamen—Fl., I (4): 1–490, Leipzig.

Johns, R. M. 1958. A New Species of *Physoderma* on *Dulichium*. Mycologia, 49: 298–299.

Karling, J. S. 1950. The Genus *Physoderma* (Chytridiales). Lloydia, 13: 29–71.

——. 1956. Unrecorded Hosts and Species of *Physoderma*. Bull. Torrey Bot. Club, 83: 292–299.

[6] Recent work has shown in another *Physoderma* that zoospores from resting spores can give rise either to endo- or epibiotic stages, as will be explained in a forthcoming paper.

Sparrow, F. K. 1952. Phycomycetes from the Douglas Lake Region of Northern Michigan. Mycologia, **44**: 759–772, 1 fig.

——. 1956. Observations on Chytridiaceous Parasites of Phanerogams. V. The Occurrence of *Physoderma butomi* and *P. vagans* in the United States. *Ibid.*, **48**: 765–766.

——. 1957a. Observations on Chytridiaceous Parasites of Phanerogams. VII. A *Physoderma* on *Lycopus americanus*. Amer. J. Bot., **44**: 661–665, 26 figs.

——. 1957b. Observations on Chytridiaceous Parasites of Phanerogams. VI. Resting Spore Germination in *Physoderma* (*Urophlyctis*) *pluriannulatum*. Mycologia, **49**: 426–429, 1 fig.

——, and R. M. Johns. 1959. Observations on Chytridiaceous Parasites of Phanerogams. IX. Epibiotic Sporangial Stages of *Physoderma* Collected in the Field. Arch. f. Mikrobiol., **34**: 93–102, 29 figs.

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BREVILEGNIELLA KERATINOPHILA GEN. NOV., SP. NOV.

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The fungus described in this paper was isolated on human hair from a soil sample taken from The University of Michigan Campus in November 1959. It appears to be identical with one described by Sparrow (1957) from Great Britain as an unidentified *Brevilegnia* and has since been recovered from his original English soil samples.

The soil was flooded with charcoal water and baited with sterile hair in 10 cm. Petri dishes and kept either at room temperature (21° C.) or at 5° C. Attempts to obtain pure cultures on artificial media were unsuccessful, and the following details have been compiled from numerous fresh-water cultures and from study of nearly 30 hanging-drop cultures. No morphological differences were observed between those kept at 21° C. and 5° C.

After considering the morphology and probable affinities of this fungus, I have felt it desirable to erect a new genus for this species.

Brevilegniella gen. nov.

Mycelium delicatum, plerumque intramatricale. Hyphae extramatricales relative brevibus, rare ramosis, maturis sporangia efformantibus; sporae exiguae, in sporangiis plerumque restantes; parthenosporae in partibus mycelii intramatricalis non mutatis formantur.

Mycelium delicate, mostly intramatrical. Extramatrical mycelium composed of relatively short, rarely branched hyphae which, at maturity, become sporangia. Asexual spores small, usually encysting within the sporangium. Resting spores formed asexually in relatively undifferentiated parts of the intramatrical mycelium.

Brevilegniella keratinophila sp. nov.

Hyphae plerumque intramatricales in capillis, irregulariter ramosae, diametrum variabiles. Hyphae extramatricales cum apicibus obtusis, breves, rare ramosae, circa 6 μ diam., 115–215(430) μ longae, maturae sporangia efformantes. Sporae in sporangiis (4)9–21(56). Sporae in sporangiis primis ut aplanosporae

[1] Contribution No. 1116 from the Botany Department, University of Michigan.

exonerantur. Sporae in sporangiis secundis relictae manent. Sporae plerumque uniseriatae, 6–7 μ diam. Parthenosporae (9)13–14(19) μ diam., in segmentis tumidis numerosis, plerumque globosae, nonnumquam irregulares, crassotunicatae (circa 1 μ). Protoplasma parthenosporam maturatam non implet, cum globula sphaerica eccentrica.

Mycelium mostly intramatrical in hair, with irregularly branching hyphae of varying diameter, eventually occupying most of the substrate; hyphae thin-walled, containing rather dense, granular protoplasm; extramatrical hyphae straight with rounded tips, usually unbranched, 115–215(430) μ long, average diameter 6 μ. Sporangia formed from the extramatrical hyphae or their distal parts, apparently without the formation of a septum; well-defined discharge papillae absent. Asexual spores 6–7 μ in diameter, uniseriate in sporangia, but sometimes in 2–3 ranks distally, (4)9–21(56) in number; spores in first-formed sporangia discharged as aplanospores, those in later-formed sporangia encysting within the sporangia. Parthenospores (resting spores) formed in the intramatrical hyphae in numerous swollen regions which may be separated from one another by cross-septa; usually spherical, less often subspherical or irregular, (9)13–14(19) μ in diameter, possessing a wall approximately 1 μ thick; contents at maturity with a clear region, within which is a spherical mass of protoplasm (6)7–9(10) μ in diameter, enveloping a large, refractive, eccentrically placed globule. All walls giving a blue or red-purple reaction with chloroiodide of zinc. Type specimens deposited at the University of Michigan Herbarium.

The presence of the fungus was usually observed macroscopically as whitish, swollen sections of the hair 8 to 12 days after baiting. Extramatrical hyphae appeared about a day after the macroscopic character was discernible, and hyphal development continued for a further 3 to 4 days, after which time most had become sporangia; few additional extramatrical hyphae developed. The growth of the intramatrical mycelium results in a disorganization of the fibers of the hair, and the attacked region loses most of its strength and rigidity. Observations could, therefore, be made by gently squashing and teasing the substrate. The mycelium could only be readily observed just prior to, and at the time of, the development of the parthenospores, since, at early stages there is little disorganization of the hair, and at maturity no protoplasmic contents can be seen in the mycelium. Parthenospores develop about a week after the initial observation of the extramatrical mycelium. The number of parthenospores formed in the swollen regions could not be accurately estimated; however, it appeared to lie between 1 and 10, mostly between 2 and 6.

The detailed development of the sporangia and aplanospores was as follows: The dense, granular, sporogenous protoplasm in the young, distal part of the hypha (which sometimes had a slightly

greater diameter) became discontinuous with the protoplasm in the more proximal region. The sporogenous protoplasm then became aggregated at regular intervals along the walls of the sporangium, which possessed a large central vacuole as found in the Saprolegniaceae. This aggregation continued until the central vacuole apparently became segmented and the spore initials were delimited. The latter became crowded toward the tip, and those behind were seen to be connected to each other by a thin central strand of protoplasm; with further differentiation a vacuole could be seen in the spore initial. This stage persisted for some minutes, often being accompanied by jerky movements of the spores suggesting the development of tensions or pressures within the sporangium. Most, but not all, of these sudden movements resulted in compression of the spores against the tip of the sporangium, sometimes to the extent of deforming them. On several occasions during this period, after the bulk of the spores had become delimited, further small aggregations of protoplasm were observed to move up to positions adjacent to those spores already formed, rounding off to form additional ones (Fig. 3). Usually each aggregation formed only 1 spore. Occasionally 2 spores were seen to coalesce during this period. At initial cleavage the sporangium tip was usually empty of spores (Fig. 2): it was never so prior to discharge (Fig. 4). Upon liberation of the spores the tip of the sporangium apparently disintegrates, and the spores are extruded at a rapid rate. These aplanospores exhibited only rocking movements and slowly sank, encysting where they came to rest (Fig. 5).

The number of spores formed in a sporangium is difficult to estimate because: (1) some may be formed in contiguous parts of the intramatrical mycelium and thus be obscured by hair material; (2) the spores are not all always delimited at the same time; and (3) the number of discharging spores is difficult to count and impracticable for statistical purposes. The remaining possibility makes use of the nonmotility of the spores, which remain associated when discharged. Such an estimate, however, could only be approximate and introduces other sorts of error. Nevertheless, the discrepancy between the two methods is worth recording and may, in some measure, indicate the frequency with which asexual spores are formed in parts of the intramatrical mycelium. Counts of spores from 88 groups of discharged spores give a range of (8)20–49(156), which may be compared with the range from 170 sporangia given in the description above for

FIGS. 1–7. Extramatrical hypha and sporangia.

spores within the sporangia. On 5 occasions I have observed empty spore cysts; all were within sporangia, and no discharge pore could be seen. The probability that many sporangia are partly intramatrical means that it is not possible to state definitely whether a septum is formed in the development of the sporangium.

From an investigation of the structure of the parthenospore, it has been possible to demonstrate that the clear region between the thick wall of the parthenospore and the mass of protoplasm is not solid, and that the protoplasm is surrounded by a very thin cellulose wall. If the hair is squashed sharply, some of the parthenospores crack. Three different types of liberation of contents by cracking could be distinguished: (1) the mass of protoplasm was forced into the mouth of the crack, where it remained as a discrete unit (Fig. 15); (2) only a small crack was formed and the protoplasm was extruded, which did not retain its shape, and a line could be seen inside the parthenospore marking the original position of the protoplasm (Fig. 14); (3) the mass of protoplasm was forced into the mouth of the crack where it ruptured, and the protoplasm dispersed, leaving an empty vesicle. On staining the preparation with chloroiodide of zinc, both the parthenospore and the vesicle stained blue, indicating that the mass of protoplasm is surrounded by an inner layer of cellulose.

Similar preparations stained for oil reserves by Sudan III indicate a positive reaction only with the protoplasm of the cracked parthenospores. It should be noted that this stain gives data which are difficult to interpret because it destroys any internal structure of the spore as well as staining any oil present.

Brevilegniella keratinophila is clearly a member of the Phycomycetes, but the absence of a flagellate asexual spore makes further classification difficult. The type of protoplasm and the development of

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1. Hypha showing aggregation of protoplasm.

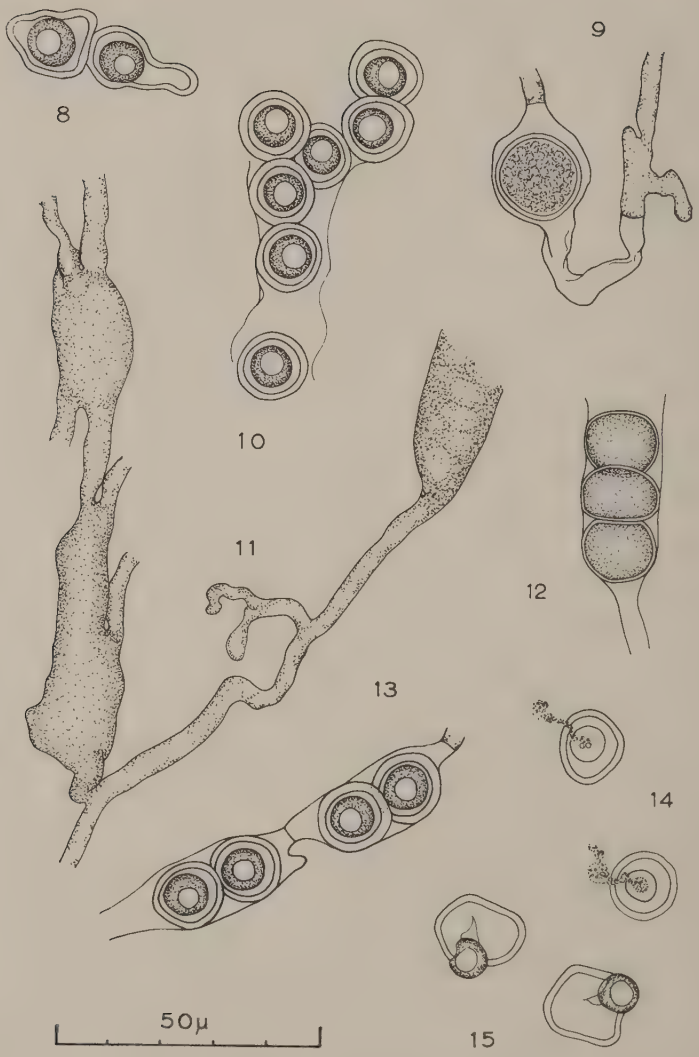
2. Spore initials soon after cleavage; note apparent absence of septum and loosely packed spores, leaving the extreme tip of the sporangium unfilled.

3. Later stage in maturation of spore initials which are moving toward the sporangium tip; note the presence of a vacuole in these spores, and that additional spores are being delimited in lower part of sporangium.

4. Spores compressed against tip of sporangium; sporogenous protoplasm in lower part of sporangium.

5. Dehisced primary sporangium with cluster of encysted spores.

6 and 7. Secondary sporangia with spores encysted within sporangia, sporangium wall disintegrating.



Figs. 8–15. Parts of intramatrical mycelium.

the asexual spores suggest that *Brevilegniella* is related to the Saprolegniales. Furthermore, the resting spore is morphologically very similar to that of *Leptolegniella keratinophilum* Huneycutt (1952),[2] who assigned his species to the Saprolegniaceae. *Brevilegniella* is also similar to *Leptolegniella* in: (1) being strongly keratinophilic and in having a mycelium which is largely intramatrical; (2) in possessing an asexual stage analogous to one found in the Saprolegniaceae; (3) in the similar diameter of the encysted asexual spores; and (4) in lacking an undoubted sexual stage.

Brevilegniella differs from *Leptolegniella* in having an asexual stage more comparable with that of *Brevilegnia* than *Leptolegnia*. It possesses distinctly swollen regions in the intramatrical mycelium and forms larger resting spores.

It may be questioned whether *Brevilegniella* and *Leptolegniella* should be retained in the Saprolegniaceae because: (1) the structure of the resting spores in these fungi is unlike that of any other member of the Saprolegniaceae; (2) the size of the encysted asexual spores in both genera is appreciably smaller than that of most other Saprolegniaceae; and (3) they differ from most Saprolegniaceae in having a largely intramatrical mycelium.

It is debatable whether these fungi are to be regarded as holocarpic or eucarpic. Since the complete mycelium of a single plant has not been seen in *Brevilegniella*, this point cannot be finally ascertained.

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8. Two irregular parthenospores, each with spherical mass of protoplasm.
9. Developing parthenospore in region of hypha cut off by cross septa.
10. Group of parthenospores within fragmentary hyphal wall.
11. Part of mycelium showing branching and three swollen regions.
12. Three immature parthenospores.
13. Two swollen regions of hypha with mature parthenospores.
14. Slightly cracked parthenospores, protoplasm dispersing revealing the inner wall of the spore.
15. Cracked parthenospores showing discrete mass of protoplasm in the mouth of the crack; note lack of any indication of the original position of the protoplasm.

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[2] I regard *Leptolegniella piligena* Ookubo and Kobayasi (1955) as properly belonging in the genus *Leptolegnia*. They state that their fungus resembles this genus both with regard to sexual and asexual structures. It has affinity to *Leptolegniella* only in the hair substrate and in the depauperate mycelium, which might be expected on this substrate.

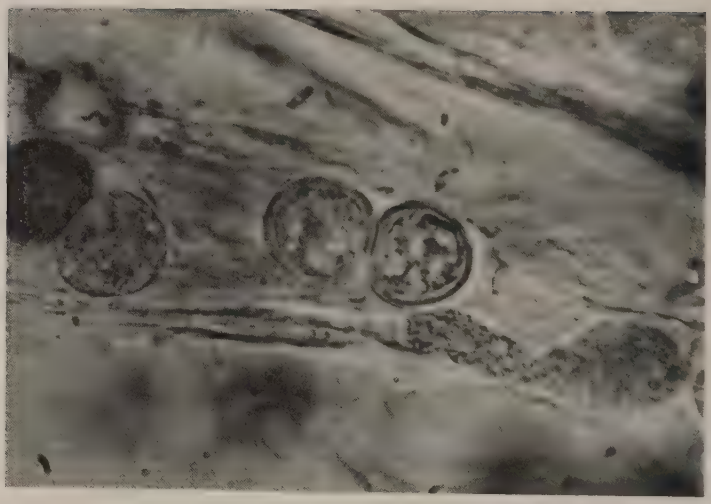
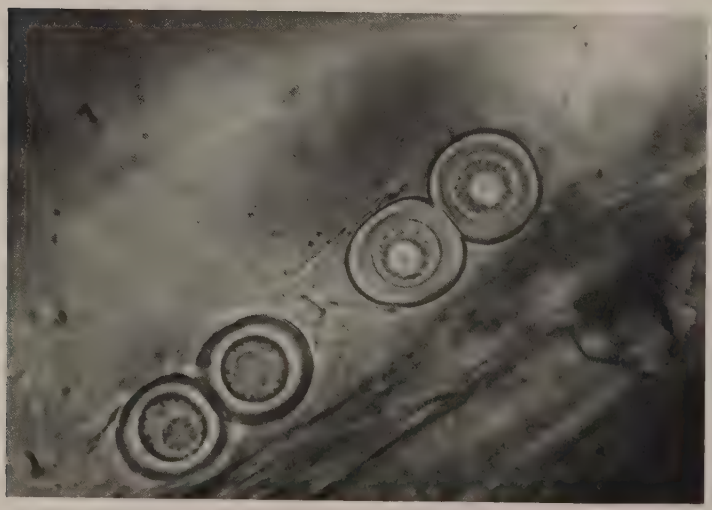


Fig. 16

50μ

Fig. 17



However, circumstantial evidence suggests that it may be holocarpic, since: (1) the extramatrical mycelium is entirely formed into sporangia; (2) no intramatrical hyphae have been observed to possess protoplasmic contents after the completion of parthenospore production; and (3) the parthenospores are so numerous as to make it unlikely that there is any part of the mycelial protoplasm which has not been used up in the formation of resting bodies.

There are indications that this may be the situation in *Leptolegniella*. Huneycutt records that the mycelium sometimes almost filled the hair. He also notes that both types of spore are formed in undifferentiated hyphae, and his illustrations indicate that they are formed in extensive segments of the mycelium. One difficulty arises from the fact that rhizoids are mentioned in his description; they are not figured and there is no information regarding their protoplasmic contents.

Huneycutt has remarked on the similarity of the resting body of *Leptolegniella* to that of *Lagenidium* and *Aphanomycopsis*. I would endorse this for *Brevilegniella* as well. However, the similarity of the cleavage of asexual spores in both genera to the Saprolegniaceae would argue against an affinity to the Lagenidiaceae.

Vishniac (1958) has recently transferred *Aphanomycopsis* from the Ectrogellaceae to her new family Haliphthoraceae, erected to include filamentous, holocarpic members of the Saprolegniales lacking a sexual stage and having a parasitic habit. If *Brevilegniella* and *Leptolegniella* are placed with *Aphanomycopsis*, then the diagnosis of the Haliphthoraceae would have to be emended to include saprophytic forms. The Haliphthoraceae may not represent a natural group, since there is recorded a difference in the appearance of the protoplasm of *Haliphthorus milfordensis* Vishniac and *Atkinsiella dubia* (Atkins) Vishniac. A final decision on this problem of affinity will have to await a comparative study of all the species involved. For the present, I would tentatively place both *Brevilegniella* and *Leptolegniella* with *Aphanomycopsis*, i.e., in the Haliphthoraceae.

Fig. 16. Developing parthenospores.

Left: two spore initials.

Center: two immature spores with thick walls; protoplasm filling the spores; note septum on right.

Right: swollen region of hypha with granular protoplasm.

Fig. 17. Two swollen regions of hypha with mature parthenospores (drawn in Fig. 13). Note the septum between the two regions.

It is a pleasure to express my gratitude to F. K. Sparrow for advice during this investigation and to A. H. Smith for the Latin diagnoses.

LITERATURE CITED

Huneycutt, M. B. 1952. A New Water Mold on Keratinised Materials. Journ. Elisha Mitchell Sci. Soc., 68: 109–112.

Ookubo, M., and Y. Kobayasi 1955. Studies on the Water Moulds on Keratinized Materials. Nagaoa, 5: 1–10.

Sparrow, F. K. 1957. A Further Contribution to the Phycomycete Flora of Great Britain. Trans. Brit. Mycol. Soc., 40: 523–535.

Vishniac, H. S. 1958. A New Marine Phycomycete. Mycologia. 50: 66–79.

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SOUTHERN AND TROPICAL POLYPORES, II*

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The Polyporaceae are chiefly wood-inhabiting fungi, and their distribution and diversity are governed partly by the available woody substrata. In the southeastern United States there is a tremendous variety of woody plants and a wide range of climatic conditions. These factors have favored the establishment of an extraordinary number of polypores, enumerated at 290 species in a recent treatment (Lowe and Gilbertson, 1961). Many of the species listed were originally described from Europe and subsequently were found in America, and additional species common to the two continents may yet be recognized. In the present paper 3 species, first described from America, are shown to be the same as species previously known only from Europe, whose names are accordingly reduced to synonymy. Additional taxonomic data are given for a fourth, inadequately known species.

Field work on which part of this paper is based was financed by the National Science Foundation.

Polyporus cerifluus Berk. and Curt.

This species, described from South Carolina in 1872, is known in North America only from the type collection. Subsequent collections so identified by Bresadola, Lloyd, and Weir, are misdeterminations; some of these have been reported in the literature (Cooke and Shaw, 1949, pp. 84 and 124 [as *P. revolutus*]; Lloyd, 1912–16, p. 322; Weir, 1917, p. 132). A European distribution has not been reported; the species occurs, however, in France and Italy, having been described from these countries by Bresadola under the name of *Polystictus revolutus*.

The sporophore of this species has no unique characteristic which readily distinguishes it from others with similar sporophores. Macroscopic characters will serve to distinguish it from *Polyporus fragilis* Fries and *P. cutifractus* Murr., which have a much softer and more distinctly fibrous context, and from *P. semisupinus* Berk. and Curt., which has pores 4–8 per mm., distinctly smaller than those of *P. cerifluus*, which are (2–) 3–4 per mm. Microscopic differences are

* The first in this series was published in these *Papers* in Volume XXXVII (1952): pp. 49–53.

needed to separate *P. ceriflavus* from *P. balsameus* Peck, which differs in having capitate cystidia.

The description by Overholts (1953, p. 290) is excellent. It was based upon the type material and is in agreement with my observations.

Poria salmonicolor (Berk. and Curt.) Cooke

This species was confused with *Poria spissa* (Schw.) Cooke by Schweinitz, and this error may have led later workers (Baxter, 1939, p. 181; Murrill, 1921, p. 96) to consider it a synonym of *P. spissa*. The sporophores of these 2 species are very similar externally, as both have orange tubes which dry to a dark purple brown or nearly black, and frequently collapse. The sporophores differ, however, in their pore size which, in *P. salmonicolor*, is 3–4 per mm., in contrast to 6–8 per mm. in *P. spissa*. Internally these species differ decidedly. The type of *P. salmonicolor*, from South Carolina, has a fibrous-fragile context composed of hyphae with usually thick walls, rare to frequent and often deformed clamp connections, mostly 4–6 μ in diameter, but more slender and often intricately branched hyphae 2–4 μ in diameter are present in variable amount; in *P. spissa* the context hyphae are septate and 3–4 μ in diameter. Spores were not seen attached to basidia in the type material, but some were found along the hymenium on isotype material (at the Farlow Herbarium); they were hyaline, smooth, oblong-ellipsoid, 3.5 × 2.5 μ and appear to be correct for this species.

This fungus appears to have been redescribed from Finland as *Physisporus aucantincus* var. *saloiscnsis* by Karsten in 1887 and as *Poria rubens* by Overholts and Lowe in 1946. The fungus is known from Finland, Ontario, New Hampshire, New York, South Carolina, Florida, Michigan, Arkansas, and British Columbia.

Polyporus semisupiniformis Murr.

This fungus, known only from the type from Mexico, externally resembles *P. semisupinus* except that it grows to somewhat larger size (Fig. 1A) and has minute pores, 9–10 per mm., distinctly smaller than those in *P. semisupinus*

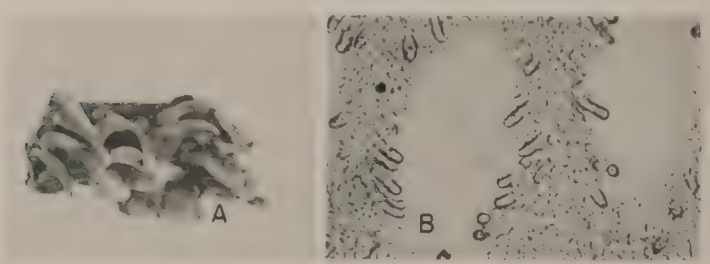

FIG. 1. Type material of *Polyporus semisupiniformis*. *A*, habit of sporophore, × 1. *B*, photomicrograph of a longitudinal section of the tubes, showing the conspicuous cystidia. About × 150.

that are 4–8 per mm. The original description does not adequately distinguish the sporophore from that of *P. semisupinus*, which is a distinct and a quite unrelated species.

Microscopic characters were not given in the original description; they are, however, highly distinctive. Cystidia are present and usually abundant (Fig. 1*B*), clavate-incrusted, and about 5–8 μ in diameter. Spores, not seen attached but numerous along the hymenial surface, are hyaline, smooth, oval to subglobose, 2.5–3.5 × 2.5 μ. The context hyphae are thick-walled to almost solid, apparently nonseptate, mostly 3–4 μ in diameter, with a very small amount of thin-walled clamped hyphae which fragment readily.

This species appears to be closely related to the fungi placed by Murrill in the genus Rigidiporus and is most similar to *R. surinamensis* (Miq.) Murr. (= *Polyporus zonalis* Berk.). The cystidia are similar to those reported for *P. zonalis* by Bose (1938, p. 683). Specific identities in this group of species are very uncertain; *P. semisupiniformis*, however, appears to be specifically distinct from *P. zonalis*.

Polyporus spraguei Berk. and Curt.

This species, reported in North America from Ontario and New Hampshire south along the Atlantic Coast to Louisiana, in the Mississippi Valley, and in Washington, has not been recorded from Europe. It occurs there on chestnut and oak in southern France, having been described as *Polyporus castaneae* by Bourdot and Galzin in 1925. Specimens from France determined as *P. castaneae* by Bourdot (Nos. 28170, 28174 at the National Fungus Collections at Beltsville, Maryland) agree in every detail with American specimens of *P. spraguei*.

LITERATURE CITED

Baxter, D. V. 1939. Some Resupinate Polypores from the Region of the Great Lakes. X. PMASAL, 24: 167–188.

Bose, S. R. 1938. The Presence of Encrusted Cystidia in the Hymenium of *Polyporus zonalis*. Mycologia, 30: 683–684.

Cooke, W. B., and C. G. Shaw. 1949. A Check List of the Polypores of the Pacific Northwest. Issued by the Department of Plant Pathology, Washington Agricultural Experiment Stations, Pullman, Wash. 183 pp., mimeo.

Lloyd, C. G. 1912–16. Mycological Writings of C. G. Lloyd, Vol. 4.

Lowe, J. L., and R. L. Gilbertson. 1961. Synopsis of the Polyporaceae of the Southeastern United States. Elisha Mitchell Soc. Jour. (in press).

Murrill, W. A. 1921. Light Colored Resupinate Polypores—III. Mycologia, 13: 83–100.

Overholts, L. O. 1953. The Polyporaceae of the United States, Alaska, and Canada. 466 pp., 132 pl. Ann Arbor: University of Michigan Press.

Weir, J. R. 1917. Montana Forest Tree Fungi. I. Polyporaceae. Mycologia, 9: 129–137.

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NOTES ON WESTERN POLYPORES

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The western United States and western Canada present a vast area in which the fungus flora is inadequately known. Over the past 10 years, J. L. Lowe and I have collected several thousand wood-rotting fungi in the West. Our knowledge of the morphology, distribution, and substratum relationships of many species of Polyporaceae has been very considerably increased by these collections, which include a large number of species of special interest. This paper presents information on two of these, *Poria rimosa* Murr. and *Trametes colliculosa* (Pers.) Lund. & Nannf. *P. rimosa* was described from New Mexico 40 years ago, but has been relatively little known ever since. *T. colliculosa* has not been previously reported from North America.

Poria rimosa

Murrill (1920a) described *Poria rimosa* from a specimen collected in New Mexico by W. H. Long and C. G. Hedgcock. Four additional collections, including one from Texas and one from Oklahoma, were reported shortly afterwards (Murrill, 1920b). No other collections of this fungus have been reported in the literature.

In his original description, Murrill gives no data on microscopic characters other than the spores, which he describes as "narrowly ovoid, . . . 5 × 2.5 μ." Baxter (1932) briefly mentions *Poria rimosa* and reports it is not known from the region of the Great Lakes, but gives no data on its morphology. Lowe (1947), after a study of the type, correctly reported the spores as ". . . broad allantoid, 4–4.5 × 1.5–2 μ," and stated that *P. rimosa* ". . . is very similar to *P. versipora* (Pers.) Rom. except for its spores." Lowe (1958), unable to confirm his original spore observation, later considered *P. rimosa* "very similar to and perhaps a form of *P. versipora* with rare clamps on the context hyphae." No other data on the morphology of *P. rimosa* has been published. Lowe subsequently was the first to observe the distinctive cystidia in the type specimen of *P. rimosa*, and he now recognizes it as a species distinct from *P. versipora*.

In addition to the 5 collections of *Poria rimosa* at the New York Botanical Garden, 8 collections, all made by Long and Hedgcock, are part of the National Fungus Collections at Beltsville, Maryland. These include specimens from Utah. Additional recent collections from Idaho, Oregon, and Arizona further extend the known distribution of *P. rimosa*. A total of 17 collections, including the type, are the basis of the following description.

Specimens examined:

Texas: On *Juniperus sabinoides*, Austin, November 16, 1911, W. H. Long, NY 12024 (specimen at BPI with same data but numbered 18642).

Oklahoma: On *Juniperus* sp. dead fallen logs, Cache, September 29, 1912, W. H. Long, no number (NY); on *J. virginiana*, Cache, September 30, 1920, W. H. Long, BPI 18653.

New Mexico: On *Juniperus monosperma*, Gila Nat. Forest, September 22, 1911, C. G. Hedgcock and W. H. Long, BPI 19223; on dead fallen *J. monosperma*, near Gila Nat. Forest, October 23, 1911, W. H. Long and C. G. Hedgcock, TYPE (NY); on *J. monosperma* stump, no locality or date, W. H. Long and C. G. Hedgcock, NY 9870; on *J. monosperma*, Gila Nat. Forest, October 23, 1911, W. H. Long and C. G. Hedgcock, NY 9884 (specimen at BPI with same data but numbered 18650); on *J. monosperma*, Pecos, W. H. Long, BPI 12737, 1913; on *J. monosperma*, Gila Nat. Forest, C. G. Hedgcock and W. H. Long, October 22, 1911, BPI 19239.

Arizona: On *Juniperus monosperma*, Silver Creek, Coronado Nat. Forest, August 23, 1958, J. L. Lowe and R. L. Gilbertson, SY-F 9106.

Utah: On *Juniperus utahensis*, Ephriam, C. G. Hedgcock, September 20, 1912 (BPI).

Idaho: On *Juniperus occidentalis*, Boulder Creek, Owyhee Co., R. L. Gilbertson, SY-F 2091 and 2092, August 2, 1958.

Oregon: On *Juniperus* sp., Prineville, John Hunt, SY-F 201, June 1955.

Poria rimosa Murr. Mycologia 12:91. 1920.

Sporophores perennial, sometimes developing as scattered patches on a cottony mycelial mat on the surface of the substratum, becoming widely effused on fallen trees, often becoming more or less cracked with age (Pl. I, Fig. 1); pore surface ivory to straw-colored, pores 5–7 per mm., angular; dissepiments thick, appearing tomentose under hand lens; tube layer ivory to straw-colored, up to 2 mm. thick; context concolorous with the tubes, soft-fibrous, up to 0.5 mm. thick; taste mild.

Context hyphae hyaline, of two types, mostly thick-walled, apparently non-septate, rarely branched, 2–3 μ in diameter, others thin-walled, with abundant clamp connections, often branched, 2–3 μ in diameter (Fig. 5B); tramal hyphae predominantly thin-walled, with clamp connections, 2–3 μ in diameter; hymenial layer hyaline, the basidia clavate, 4-spored, 10–12 × 5–6 μ; hyphal pegs present, 15–30 × 7–16 μ; cystidia scarce to abundant, not incrusted, thin-walled, subulate, 25–35 × 4–6 μ, and projecting up to 25 μ beyond the hymenium; spores hyaline, smooth, allantoid, 4–5 × 1.5–2 μ (Fig. 5*A*).

Sporophores of *Poria rimosa* have been found only on juniper, and develop on dead wood on the ground and dead standing trees. They are also found on dead branches of living trees, in which the decay appears to extend into the heartwood of the living part of the tree. A white rot is associated with sporophores of *P. rimosa*. In the advanced stages small, empty pockets develop in the wood, giving it a delicate, lacelike appearance (Pl. I, Fig. 2). The rot is similar in appearance to that caused by the common *Polyporus abietinus* Dicks. ex Fries.

As Murrill has reported (1920b), collection data with 2 of the early collections of *Poria rimosa* by Hedgcock and Long include the statement "following *Fomes texanus* rot." *F. texanus* is considered by Lowe (1957) to be a synonym of *F. robustus* Karst. and causes a yellow stringy heartrot of living junipers. Recent collections of *P. rimosa* from Idaho and Arizona were not associated with a rot of this type. A part of the specimen cited from Arizona, however, had grown over an old weathered sporophore of *F. demidoffii* (Lèv.) Cooke, one of the few other wood-rotting fungi on western junipers.

The distinctive cystidia, the typical rimose appearance of mature sporophores, and its apparent restriction to *Juniperus* characterize *P. rimosa*. Among the other cystidiate western porias that decay coniferous wood, *P. luteoalba* Karst. is most similar to *P. rimosa*. *P. luteoalba* differs in having larger, heavily incrusted, thick-walled cystidia, and also occurs on other conifers, in contrast to *P. rimosa*, known only on juniper.

Trametes colliculosa

Trametes colliculosa has been known in Europe since the time of Persoon, who described it in 1825. It appears to have been a lost species for more than a century as evidenced in 1890 by Romell's describing it as *Polyporus albo-carneo-gilvidus*. Romell, however, later (1926) recognized his species to be a synonym of the older Persoonian name. It has been subsequently reported from various parts of Europe by Pilát (1936–42) and Bondarzew (1953).

During August and September of 1958, 4 collections of *Trametes colliculosa* were made by J. L. Lowe and R. L. Gilbertson near the Research Station of the American Museum of Natural History in the Chiricahua Mountains of southeastern Arizona. No other collections of this fungus from North America have been found in herbaria or reported in the literature. Direct comparison of the Arizona specimens and 2 European specimens identified by Romell shows them to be strikingly similar, including the distinctive spores. They differ only in that the European specimens show a tendency to develop a perennial habit and the Arizona specimens all have a single layer of tubes. There appears to be no doubt that they represent the same species. An interesting distribution pattern is presented by the occurrence of *T. colliculosa* in the two widely separated and ecologically different areas.

The following description is based upon 4 collections from Arizona and 2 from Sweden.

American specimens studied:

Arizona: On dead oak, Rucker Canyon, Cochise Co., Sept. 7, 1958. J. L. Lowe and R. L. Gilbertson, SY-F 9741, 9812, and 9803; on dead oak, Cave Creek, Cochise Co., Aug. 22, 1958. J. L. Lowe and R. L. Gilbertson, SY-F 9069. *Trametes colliculosa* (Pers.) Lund & Nannf., Fungi Suec. exs. No. 450. 1937. Not *Trametes colliculosus* Berk. 1847.

Polyporus colliculosus Pers., Myc. Eur. 2:103. 1825.

Polyporous albo-carneo-gilvidus Rom., Fungi Exsiccati Praes. Scand., No. 17. 1890.

Sporophores annual in our specimens, resupinate, effused up to 15 cm., usu-

ally appearing nodulose or irregular because of the uneven configuration of the bark on which they develop (Pl. I, Fig. 3); margin fertile or narrowly sterile, concolorous with the pore surface, even; pore surface cream to light buff, the pores circular to angular, 2–3 per mm.; dissepiments thick, entire, finely tomentose; context cream to light buff, soft-fibrous, up to 5 mm. thick; tube layer continuous and concolorous with the context, up to 3 mm. thick; feltlike, light buff mycelium present in bark and decayed wood beneath sporophores.

Context hyphae hyaline, of two types, mostly thick-walled, nonseptate, occasionally branched, 2–4 μ in diameter, others thin-walled, clamped, 2–4 μ in diameter, others thin-walled, clamped, 2–4 μ in diameter (Fig. 5*C*); basidia 4-spored, 16–20 × 9–10 μ; spores hyaline, appearing minutely echinulate because of pitted exospore, ellipsoid to cylindric-ellipsoid, 12–17 × 5–7 μ (Fig. 5*D*).

All reports of this fungus in Europe list oak as the substratum. The Arizona specimens are all from oak and were on dead standing trees or dead fallen trees with the bark still attached. The decay associated with *Trametes colliculosa* is of the uniform white type and in the advanced stages becomes chalky in consistency with the ray tissue apparently completely replaced by mycelium of the fungus (Pl. 1, Fig. 4). Cream-colored mycelium is usually conspicuous in the bark under the fruiting bodies and between the bark and wood.

The very large spores that appear minutely echinulate are diagnostic for *Trametes colliculosa*. *T. heteromorpha* (Fries) Bres. and *T. campestris* Quél. are similar macroscopically but have smooth spores.

Collecting in Arizona in 1958 was done while I was assisting J. L. Lowe on a project supported by a grant from the National Science Foundation. Collections of *Poria rimosa* in Idaho were made while I was employed by the College of Forestry, University of Idaho.

The loan of specimens and the use of herbarium facilities of the New York Botanical Garden (NY) and the National Fungus Collections at Beltsville, Maryland (BPI) are gratefully acknowledged. Specimens in the herbarium of the State University of New York College of Forestry at Syracuse University (SY-F) were also used in this study.

Material from the Arizona, Idaho, and Oregon collections cited has been deposited in herbaria of the following institutions: National Fungus Collections at Beltsville, Maryland; New York Botanical Garden; Farlow Cryptogamic Herbarium; Forest Disease Laboratory, Beltsville; University of Michigan; Washington State University; University of Arizona; Museum National d'Histoire Naturelle, Paris; Royal Botanic Gardens, Kew, England; and the Riksmuseet, Stockholm.

LITERATURE CITED

Baxter, D. V. 1932. Some Resupinate Polypores from the Region of the Great Lakes. III. PMASAL, 15: 191–228.

Bondarzew, A. 1953. Polyporaceae of the European Part of the Union of SSR and of the Caucasus. 1106 pp. Leningrad. (In Russian.)

Lowe, J. L. 1947. Studies in the Genus Poria. II. White and Brightly-colored Type Material. Lloydia, 10: 45–59.

—— 1957. Polyporaceae of North America. The Genus Fomes. N.Y.S. Coll. Forestry Tech. Publ. 80.

—— 1958. The Genus Poria in North America. Lloydia, 21: 100–114.

Murrill, W. A. 1920a. Light-colored Resupinate Polypores. I. Mycologia, 12: 77–92.

—— 1920b. Light-colored Resupinate Polypores. II. Mycologia, 12: 299–308.

Pilát, A. 1936–42. Polyporaceae I–III. *In* Kavina, C., and A. Pilát, Atlas des Champignons de l'Europe, Tome 3.

Romell, L. 1926. Remarks on Some Species of Polyporus. Svensk. Bot. Tidskr., 20: 1–24.

PLATE I

FIGS. 1–4. Sporophores and associated rot of *Poria rimosa* and *Trametes colliculosa*. Fig. 1, sporophore of *P. rimosa* (R. L. Gilbertson, 2092); Fig. 2, white pocket rot associated with *P. rimosa* (R. L. Gilbertson, 2092); Fig. 3, sporophore of *T. colliculosa* (J. L. Lowe and R. L. Gilbertson, 9069); Fig. 4, uniform white rot associated with *T. colliculosa* (J. L. Lowe and R. L. Gilbertson, 9069); all × 1.

PLATE I

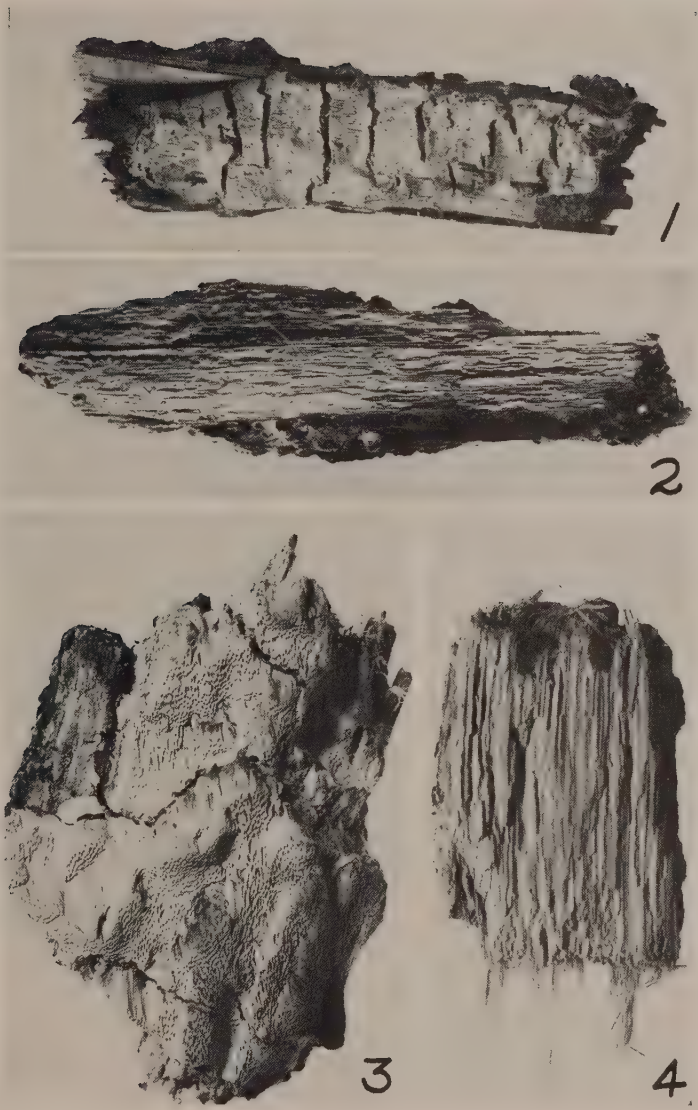
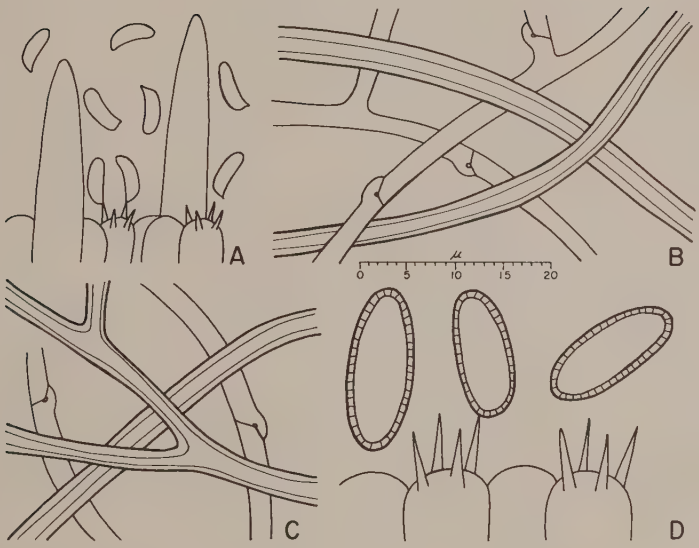


PLATE I (*Continued*)

FIG. 5. *A–D*. Microscopic features of *Poria rimosa* and *Trametes colliculosa*. *A*, basidia, cystidia, and spores of *P. rimosa*; *B*, context hyphae of *P. rimosa*; *C*, context hyphae of *T. colliculosa*; *D*, basidia and spores of *T. colliculosa*.

PLATE I (*Continued*)



Papers of the Michigan Academy of Science, Arts, and Letters
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FORESTRY

JACK PINE GEOGRAPHIC VARIATION—FIVE-YEAR RESULTS FROM LOWER MICHIGAN TESTS

JOHN L. AREND, NORMAN F. SMITH, STEPHEN H. SPURR, AND JONATHAN W. WRIGHT[1]

Introduction

Jack pine (*Pinus banksiana* Lamb.) is one of three pine species native to the Lake States. It is the most important pine species in Michigan in terms of acreage of natural stands and production of pulpwood and lumber.

Jack pine is a medium-sized tree, commonly attaining a mature height of 55 to 65 feet and a diameter of 8 to 10 inches, the maxima being 100 feet tall and 25 inches diameter breast high (Rudolf, 1958). If open-grown, it is apt to be crooked and very branchy. It rarely produces high-quality sawlogs. Three characteristics, however, make it a continued mainstay to Lake States forest industries: ability to grow on dry, sandy soils; early rapid growth; and suitability for pulp.

Because of its importance and convenience as a test organism, jack pine was one of the first Lake States species chosen for tree improvement work. Provenance testing to determine the major variation patterns loomed large in this work. The first provenance testing was started by the University of Minnesota in 1940 when seeds were collected from 32 different localities in the eastern United States and Canada. The resulting seedlings were outplanted in Austin and Cloquet, Minnesota, in 1943 and 1944. The plantings have been measured and scored at intervals since 1948 (Schantz-Hansen and Jensen, 1952, 1954; Schoenike et al., 1959). A smaller provenance study was started by Rudolf of the Lake States Forest Experiment Station in 1943 when

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stock of 9 different origins was outplanted in Wexford County, Michigan.

The third and most comprehensive study of geographic variation in jack pine was begun in 1950 by the Lake States Forest Experiment Station and the University of Minnesota. Seed was collected from 29 seed sources in the Lake States region, and the seedlings were outplanted by coöperators at 17 different locations in Minnesota, Wisconsin, and Michigan. Eight of the provenances are also being tested in Massachusetts and 16 in Ontario. The first report on this 29-origin study, published by Stoeckeler and Rudolf (1956), summarized their observations on fall coloration in the nursery. The present paper is the second report and summarizes the performances of the trees 5 years after outplanting in the 3 test plantings in Lower Michigan.[2]

Methods

Work plans.—A detailed work plan for the study was prepared in 1953 by P. O. Rudolf of the Lake States Forest Experiment Station and T. Schantz-Hansen of the University of Minnesota. It covered the details of seed handling, nursery procedure, outplanting design, outplanting methods, and measurement methods. The plan was followed up to and including the making of the fifth-year measurements, but additional statistical techniques were introduced in the analyses of the data. Thus, except for the statistics, these data should be comparable to those obtained from the other 14 outplantings in the Lake States.

Seed procurement and handling.—In 1951, foresters at 29 locali-

[2] In addition to the published reports, mimeographed progress reports have been distributed to coöperators.

This is a coöperative project undertaken by the Lake States Forest Experiment Station, Michigan Department of Conservation, The University of Michigan, and Michigan State University. P. O. Rudolf and T. Schantz-Hansen planned and started the studies. J. H. Stoeckeler handled the nursery sowing, and he and P. O. Rudolf were largely responsible for the proper numbers of well-labeled trees reaching the planting sites in time. Their responsibility includes all 17 Lake States plantings. We express our appreciation to the many who have assisted, especially to T. Aakala, Burton V. Barnes, R. M. Godman, Paul Guilkey, Fred Haskins, N. J. Karsten, J. Lockwood, S. R. Miller, W. Miller, D. Smock, R. A. Ralston, R. Turunen, J. Vander Sys, and R. M. Wolfe; and to Burton V. Barnes, Albert Foulger, and Frank W. Kearns, who helped in the statistical analysis. Mich. Agr. Expt. Sta. Jour., Art. No. 2721.

TABLE I

Location and Climatic Data of the 29 Seed-Source Areas

(From Stoeckeler and Rudolf, 1956)

Collection No.	County	Latitude (degrees)	Longitude (degrees)	Average Annual Precipitation (ins.)	Frost-free Days per Year (no.)	Average January Temperature (°F.)
		Minnesota				
1589	Itasca	47.00	94.00	24	125	5
1590	Cass	47.34	94.52	24	130	7
1591	Itasca	47.55	93.73	24	120	5
1592	Lake	47.75	91.23	28	115	10
1593	Cook	48.00	90.33	30	125	14
1594	St. Louis	48.03	92.42	26	105	5
1595	Pine	45.95	92.55	27	130	10
1596	Pine	46.30	92.93	26	125	9
1597	Becker	47.08	95.47	24	110	4
1600	Cass	46.75	93.97	26	130	6
1601	Beltrami	47.48	95.00	22	115	5
1602	Itasca	47.75	93.28	24	105	6
		Wisconsin				
1604	Douglas	46.34	91.73	28	120	10
1605	Bayfield	46.75	90.95	28	130	13
1606	Forest	46.02	88.93	31	95	12
1607	Oneida	45.82	89.17	31	105	11
1608	Burnett	45.92	92.03	28	125	10
1609	Marinette	45.28	92.55	30	125	14
1610*	Oneida	45.75	89.93	31	125	10
1611	Wood	44.45	89.72	32	130	13
		Michigan				
1612	Gogebic	46.22	89.20	32	80	12
1613	Ontonagon	46.56	89.02	32	85	15
1614	Alger	46.24	86.62	32	90	15
1615	Chippewa	46.26	84.84	30	140	15
1616	Manistee	44.26	86.26	30	145	22
1617	Ogemaw	44.34	84.12	28	95	19
1618	Alpena	45.00	83.54	30	135	19
1620	Grand Traverse	44.62	85.37	28	145	18
1621	Luce	46.60	85.38	30	140	16

* Climate at Hugo Sauer Nursery is similar to that given for the area where this collection was made.

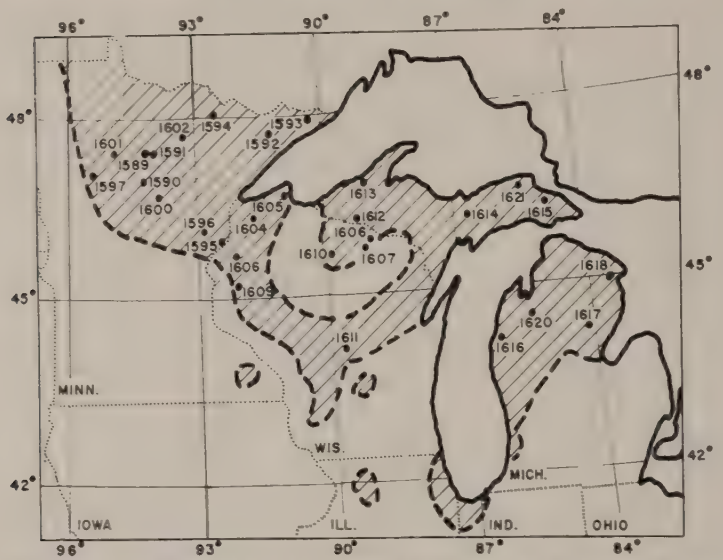

FIG. 1. Locations of the 29 seed-source areas. The boundary of the natural range of jack pine is outlined with a dashed line.

ties in the Lake States were asked to collect approximately 1 bushel of cones from several average trees in a stand in their vicinity. The collections, made in the winter of 1951–52, were shipped to a central location for extraction and testing of germination per cent. The locations and climatic characteristics of the collection localities are given in Table I and Fig. 1.

The 30th seedlot, designated as "Huron" and obtained in the same general area as provenances 1617 and 1618, consisted of ordinary commercial seed being used at that time for reforestation in the Lower Michigan National Forest.

Nursery handling.—The seed from the 29 sources was sown in the Hugo Sauer Nursery at Rhinelander, Wisconsin. Drills were spaced 4 inches apart, and the density was designated to produce 25 to 30 trees per square foot. There was no thinning. Although each seed source was sown in several different parts of the nursery, the planting stock for each provenance was derived mainly from one nursery plot.

The 30th seed source was from a general seed collection and was grown in the U. S. Forest Service's Chittenden Nursery at Wellston, Michigan.

Outplanting.—Three outplantings were established in Michigan's Lower Peninsula. Their sites are described below.

1. Fife Lake State Forest, Grand Traverse County
   44° 33′ N., 35° 28′ W.
   Elevation: 1,066 feet
   Soil: Grayling sand
   Aspect: Flat
   Average January and July temperatures: 19° and 68° F.
   Length of growing season: 97 days
   Annual precipitation: 30 inches
   Planted: May 3–5, 1954
2. Au Sable State Forest, Crawford County
   44° 32′ N., 84° 16′ W.
   Elevation: 1,190 feet
   Soil: Grayling sand
   Aspect: Flat
   Average January and July temperatures: 17° and 67° F.
   Length of growing season: 96 days
   Annual precipitation: 28 inches
   Planted: May 3–5, 1954
3. University of Michigan Biological Station, Emmet County
   45° 33′ N., 84° 15′ W.
   Elevation: 690 feet
   Soil: Lake Algonquin lake bed, Kalkaska sand
   Aspect: Flat
   Average January and July temperatures: 19° and 65° F.
   Length of growing season: 99 days
   Annual precipitation: 31 inches
   Planted: April 29–30, 1954

The planting methods were similar at the three locations. Single furrows 6 feet apart constituted the ground preparation. The 2-0 trees were planted in slits placed 6 feet apart in the bottoms of the furrows. The slight (4 to 6 per cent) first-year losses were replaced at the start of the second growing season with 2-0 trees from identical seed sources.

Experimental design.—The same randomized complete block design was used in all three plantings. At each location, every seed origin was represented by four 8 x 8 = 64-tree plots, one plot being located in each of 4 replicates. The replicates consisted of 5 x 6 = 30-plot

rectangles. Two rows of the "local" stock were planted around each set of 4 replicates. A single planting contained

30	×	4	×	64	+	720	=	8,400 trees.
origins		replicates		trees per plot		border trees		

The area occupied by each planting was 420 feet x 500 feet = 210,000 sq. ft. or 4.8 acres.

Measurements.—The plantings were measured in the autumns of 1954, 1955, and 1958; only the 1958 measurements are included in this paper.

The measurements were made by two-man crews who made a single traverse through a planting on each measurement date. On this traverse they recorded the height (to the nearest tenth of a foot) of each tree and noted whether or not it possessed any one of approximately 125 characteristics listed in the work plan. These data were recorded in squares on printed plot maps, one of these maps being used for each of the 120 plots in a planting.

In the Au Sable planting the observer and recorder alternated positions on successive plots. Whether this introduction of variable observer bias lowered the precision of the observations is unknown.

Statistical Analysis of Data

Plot means were used in all statistical analyses. Differences among means that could occur less than 5 per cent of the time by chance alone were evidence of genetic differences (5 per cent level). Differences so great that they could occur less than 1 per cent of the time by chance were noted. Every statement as to presence or absence of genetic differences among provenances is based either on a variance or binomial analysis.

The degrees of freedom used for a variance analysis of a single characteristic in a single planting were as follows:

Source	*Degrees of Freedom*
Total	119
Provenance	29
Replication	3
Error	87

To study a single characteristic in all three plantings the following degrees of freedom were used:

Source	*Degrees of Freedom*
Total	359
Provenance	29
Replication	
Within plantings	9
Between plantings	2
Provenance × planting	58
Error	261

Percentage values were inserted directly into analysis-of-variance computations even though angular transformations are usually recommended in such cases. The particular percentage arrays with which we were concerned proved upon preliminary examination to be approximately normally distributed, indicating that transformations were unnecessary.

Duncan's (1955) multiple-range test was used in conjunction with the analyses of variance to determine the significance of the differences between individual provenances.

Binomial analyses were used to advantage for the analysis of some rare present-absent characters. The methodology was as follows. If a character was present on 27/120 = 9/40 of the plots, the probability of presence (p) is 9/40 and that of absence (q) is 31/40, and the probabilities of presence on 4, 3, 2, 1, or 0 plots respectively of a provenance are given by the expansion of the binomial $(p + q)^4 = (9/40 + 31/40)^4$. The probability that the character is present on all four plots of a provenance is given by the first term ($p^4 = (9/40)^4 = .00256$), and the probability that at least one provenance (out of a total of 30) would have the character present is .00256 x 30 = .0768. Therefore, the occurrence of the character on all four plots of one provenance is not significant in this case since it is expected to occur by chance more than 5 per cent of the time.

Results

Mortality.—At the end of the first growing season after spring planting (1954), mortality was approximately 4.3, 4.3, and 5.1 per cent in the Fife Lake, Au Sable, and Biological Station plantings, respectively. These dead trees were replaced in the spring of 1955

with 2-0 planting stock from the same seed sources. In the ensuing 4 years approximately 1.0, 4.6, and 5.5 per cent of trees died in the three plantings, respectively.

Because most of this mortality was a function of transplanting damage and since there was no replication regarding transplanting damage (all trees of one provenance were lifted from the same part of the nursery at the same time and were handled similarly), the differences in mortality among provenances are considered to be without genetic significance.

At the end of the fifth growing season, there was no consistent difference between the original trees and their replacements. Therefore, all trees living in 1958 were treated similarly in subsequent analyses.

Height.—The average 1958 heights were 5.06 feet, 4.75 feet, and 4.07 feet for the Fife Lake, Au Sable, and Biological Station plantings, respectively.

The plot means were subjected to analysis of variance separately and combined (Tab. II). In each plantation the differences due to provenance and replication were statistically significant at the 1 per cent level. The provenance F values show the general level of precision in the three plantings—the Fife Lake planting was the most precise and gave the most information. This superiority of the Fife Lake planting is probably due to a combination of factors—better planting techniques, greater uniformity of the site, and generally more favorable growth conditions.

The plantation-provenance interaction was not significant (Tab. II). This means that slight differences in relative performance of different provenances in different plantations should be disregarded in this data. It also means that the data from the three plantings (Tab. III) can be combined and considered to have come from one 12-replication planting (Tab. IV). When this was done, error of a provenance mean was lower and the efficiency of Duncan's multiple-range test was higher than for any one of the three plantings analyzed separately.[3]

[3] It is often customary to publish provenance means separately by plantation so that a local reader could determine which provenance did best under his conditions. Such detailed reporting is not only unnecessary but may be misleading if the provenance-plantation interaction is not significant because in that case the overall provenance mean is a better indicator of performance at a local site than is a less accurately determined local mean.

TABLE II

ANALYSES OF VARIANCE OF THE 1958 HEIGHT AND WHITE-PINE WEEVIL DATA FOR THE THREE TEST PLANTATIONS CONSIDERED SEPARATELY AND TOGETHER

Source of Variation	Separate Analyses				Combined Analyses	
	D.F.	F value				
		Fife Lake	Au Sable	Biological Station	D.F.	F value
Height measurements						
Provenance	29	5.68*	4.06*	2.01*	29	9.48*
Replication						
Within plantation	3	5.95*	10.33*	12.75*	9	9.95*
Between plantations	—	—	—	—	2	446.34*
Provenance × plantation	—	—	—	—	58	0.84
Error	87	—	—	—	261	—
Amount of weeviling						
Provenance	29	1.89†	2.26*	1.66†	29	3.83*
Replication						
Within plantation	3	2.65	2.59	14.65*	9	7.54*
Between plantations	—	—	—	—	2	49.72*
Provenance × plantation	—	—	—	—	58	0.99
Error	87	—	—	—	261	—

* Significant at 1 per cent level.
† Significant at 5 per cent level.

The two seedlots from the western part of Lower Michigan (Region A) grew significantly faster than any of the others (Tab. IV). Next were two seedlots from the eastern part of Lower Michigan (Region B). Then came jack pines from Region D, which includes Minnesota, Wisconsin, and a small portion of Michigan's Upper Peninsula just over the Wisconsin border. Significant random differences in growth within that region were noted, the fast-growing ones (1601, 1610, 1608, and 1611) being from very different parts of Minnesota and Wisconsin. At the bottom of the list are the four seedlots from Region C, Upper Michigan. They were nearly 20 per cent

TABLE III

AVERAGE HEIGHTS OF JACK PINE PROVENANCES IN EACH EXPERIMENTAL PLANTING (IN FEET)

Region and Provenance*	Experimental Planting		
	Fife Lake	Au Sable	Biological Station
B "Huron"	5.68	4.53	5.37
A 1620	5.71	4.71	5.04
A 1616	5.57	4.63	5.26
B 1617	5.46	4.35	4.98
B 1618	5.25	4.52	4.98
D 1601	5.28	4.15	5.24
D 1610	5.27	4.26	5.03
D 1608	5.26	4.20	4.86
D 1611	5.06	4.13	4.99
D 1595	5.21	4.19	4.75
D 1589	5.04	4.24	4.78
D 1604	5.21	3.99	4.86
D 1609	5.15	3.92	4.82
D 1590	4.85	4.13	4.89
D 1597	5.09	3.94	4.82
D 1607	4.98	3.89	4.91
D 1594	4.97	3.92	4.89
D 1592	5.08	3.97	4.72
D 1612	5.09	3.92	4.73
D 1596	4.97	3.98	4.77
D 1600	5.02	3.72	4.83
D 1593	4.90	3.91	4.72
D 1606	4.91	3.85	4.69
D 1591	4.80	3.96	4.64
D 1602	4.90	3.90	4.58
C 1615	4.80	3.83	4.64
C 1621	4.56	3.89	4.78
C 1614	4.66	3.93	4.60
C 1605	4.47	3.73	4.69
C 1613	4.55	3.79	4.43

* Regions are as follows: A = western Lower Michigan; B = eastern Lower Michigan; C = Upper Michigan; D = Minnesota and Wisconsin. D also includes one seed source from Upper Michigan just over the Wisconsin border.

TABLE IV

AVERAGE HEIGHTS OF THE JACK PINE PROVENANCES IN THE FIFE LAKE, AU SABLE, AND BIOLOGICAL STATION PLANTINGS

Region and Provenance*	Height in Feet	Significance at the 5 per cent level	Significance at the 1 per cent level
B "Huron"	5.20	†	
A 1620	5.16		
A 1616	5.16		
B 1617	4.94		
B 1618	4.91		
D 1601	4.90		
D 1610	4.85		
D 1608	4.78		
D 1611	4.73		
D 1595	4.72		
D 1589	4.69		
D 1604	4.69		
D 1609	4.64		
D 1590	4.61		
D 1597	4.61		
D 1607	4.59		
D 1594	4.59		
D 1592	4.59		
D 1612	4.57		
D 1596	4.56		
D 1600	4.52		
D 1593	4.51		
D 1606	4.48		
D 1591	4.47		
D 1602	4.46		
C 1615	4.42		
C 1621	4.41		
C 1614	4.37		
D 1605	4.29		
C 1613	4.26		

Provenance mean = .0785

* Regions are as follows: A = western Lower Michigan; B = eastern Lower Michigan; C = Upper Michigan; D = Minnesota and Wisconsin. D also includes one seed source from Upper Michigan just over the Wisconsin border.

† Bars connect provenances which are not significantly different from each other.

shorter than those originating south of the Straits of Mackinac and differed significantly from nearly all those from Minnesota and Wisconsin.

Resistance to white-pine weevil (*Pissodes strobi* (Peck)).—The white-pine weevil was the most damaging insect in the plantings. The percentages of trees damaged by this insect during 1958 are shown in the following tabulation.

Plantation	*Weeviled Trees (per cent)*
Fife Lake	23.2
Au Sable	30.8
Biological Station	16.8

Analyses of variance of the percentages showed statistically significant differences among provenances (at the 5 per cent level for the Fife Lake and Biological Station plantings and at the 1 per cent level for the Au Sable and combined plantings) and among plantings (Tab. II). The provenance-plantation interaction was not significant; and therefore the data for all three plantations were combined for the multiple-range analysis.

The genetic differences in resistance to weeviling appear to be randomly distributed, provenances from Region D being among the least heavily and most heavily weeviled (Tab. V). However, because of the low statistical precision possible with enumeration data of this sort, it is unwise to say definitely whether the variation pattern is random or systematic.

Resistance to pitch twig moth (*Petrova comstockiana* (Fern.)).—The pitch twig moth was the second most damaging insect in the test plantings. It damaged 9.3 per cent, 7.8 per cent, and 30.0 per cent of the trees in the Fife Lake, Au Sable, and Biological Station plantings, respectively. The differences among provenances were not significant.

Resistance to bark beetles (*Pityophthorus* spp.).—About 10 per cent of the trees in the Fife Lake plantation were damaged by bark beetles, but no damage occurred in the other two areas. The differences among origins on the Fife Lake plantation were significant at the 1 per cent level (Tab. VI). There was no apparent correlation between geographic origin and degree of susceptibility, some provenances from all regions suffering relatively heavy attacks.

Resistance to red-headed pine sawfly (*Neodiprion lecontei*

TABLE V

RELATIVE SUSCEPTIBILITY OF JACK PINE PROVENANCES TO THE WHITE-PINE WEEVIL (*Pissodes strobi* (Peck))

Region and Provenance*	Trees Affected, in Per Cent	Significance at the 5 per cent level	Significance at the 1 per cent level
D 1606	15.1	†	
D 1593	15.3		
D 1621	15.3		
D 1592	16.5		
D 1602	17.8		
D 1601	18.0		
D 1591	18.0		
B "Huron"	19.0		
A 1620	19.6		
D 1607	20.8		
C 1615	21.4		
D 1594	21.4		
D 1605	21.8		
D 1590	23.0		
D 1589	23.3		
A 1616	23.6		
B 1618	23.7		
B 1617	23.8		
D 1595	24.6		
C 1613	25.5		
D 1600	26.4		
C 1614	26.8		
D 1597	27.6		
D 1596	28.4		
D 1609	29.4		
D 1611	29.4		
D 1604	31.3		
D 1612	32.5		
D 1608	32.7		
D 1610	35.9		

* Regions are as follows: A = western Lower Michigan; B = eastern Lower Michigan; C = Upper Michigan; D = Minnesota and Wisconsin. D also includes one seed source from Upper Michigan just over the Wisconsin border.

† Bars connect provenances which do not differ significantly.

TABLE VI

DIFFERENCES IN RESISTANCE TO BARK BEETLES (*Pityophthorus* spp.) IN THE FIFE LAKE PLANTATION

Region	Provenance	Trees Attacked, in Per Cent	Significance at the 5% level	Significance at the 1% level
D	1593	5.1		
D	1610	5.1		
D	1596	6.2		
D	1590	7.0		
D	1607	7.4		
B	"Huron"	7.8		
C	1621	7.8		
D	1600	7.8		
D	1611	7.8		
D	1606	8.2		
D	1589	8.2		
D	1609	8.6		
B	1617	9.4		
D	1521	9.8		
A	1620	9.8		
D	1604	9.8		
D	1608	10.9		
D	1595	10.9		
D	1605	11.3		
D	1597	12.1		
D	1601	12.1		
D	1592	12.9		
B	1618	12.9		
C	1613	13.3		
C	1614	13.3		
D	1594	13.3		
D	1602	14.4		
D	1612	14.8		
C	1615	16.8		
A	1616	17.2		

Summary of analysis of variance

Source	Degrees of freedom	F value
Provenance	29	1.95*
Replication	3	5.61*
Error	87	—

* Significant at the 1 per cent level.

‡ Bars connect provenances that do not differ significantly.

(Fitch)).—In 1958 damage from sawflies (most of them believed to be the red-headed pine sawfly, which eats new as well as old needles) was as follows:

Fife Lake planting—196 trees damaged
Au Sable planting—116 trees damaged
Biological Station—123 trees damaged planting

Analyses of variance on the data from the individual plantings would not be valid because of the large numbers of plots in which the mean percentage of damage was zero. However, the combined data for the three plantings, which did not have this limitation, were subjected to an analysis of variance. This showed the presence of significant differences among provenance means (Tab. VII).

Resistance to oak-pine gall rust (*Cronartium cerebrum* Hedgc. & Long).—In the Au Sable planting, damage was noted on 36 trees on 27 of the 120 plots. All four plots of provenance 1592 contained cankers. This does not constitute evidence of genetic differences since the probability of all four plots of one provenance being damaged, when there are 30 provenances, is greater than .05.

Other characteristics.—Occasional trees were damaged by snow, drought, budworms, and deer in all plantings. In the Au Sable plantation 10 per cent of the trees bore cones. The between-provenance differences in these characteristics were not significant.

Discussion

Processes governing differentiation in jack pine.—Climate is normally considered to cause genetic differentiation. This study shows no perfect correlation between climate of origin and genetics characteristics of jack pine. The fastest growing jack pines planted in northern Lower Michigan came from the four seed sources in this area. However, there was a slight but significant difference in early height growth from the two seed sources in the western part compared to the two from the eastern part of northern Lower Michigan where the climate is similar. The next fastest growing jack pine came from seed sources in northern Wisconsin and Minnesota where the climate is quite different from that of Lower Michigan. The slowest growing jack pine came from seed sources in Upper Michigan; here again the climate differs not only from that of the northern Lower Peninsula but also from the Minnesota climate. These facts alone indicate that

TABLE VII

DIFFERENCES IN RESISTANCE TO SAWFLIES, BELIEVED TO BE MOSTLY THE RED-HEADED PINE SAWFLY (*Neodiprion lecontei* (Fitch)).

Region	Provenance	Trees Attacked, in Per Cent	Significance at the 5 per cent level
D	1592	2.3	
B	"Huron"	2.3	
D	1611	2.7	
D	1608	3.1	
A	1616	3.1	
D	1601	3.5	
D	1593	3.5	
C	1621	3.9	
D	1597	3.9	
D	1590	4.3	
A	1620	4.3	
C	1614	4.7	
D	1604	4.7	
D	1596	4.7	
C	1613	5.1	
C	1615	5.4	
D	1594	5.8	
D	1589	6.2	‡
D	1591	6.2	
D	1595	6.2	
D	1605	6.2	
D	1607	6.2	
D	1609	6.6	
D	1602	7.4	
D	1600	7.8	
B	1618	8.6	
D	1619	8.6	
B	1617	9.4	
D	1612	9.4	
D	1606	13.3	

Summary of analysis of variance

Source	Degrees of freedom	F value
Provenance	29	1.77*
Plantation	2	8.57†
Error	58	—

* Significant at the 5 per cent level.

† Significant at the 1 per cent level.

‡ Bars connect provenances that do not differ significantly.

climate in the region of origin is a factor governing the genetic differentiation of jack pine but not an all-controlling one.

Population structure is the other important factor affecting genetic differentiation in these populations. Consider the situation on either side of the 4.4-mile-wide Straits of Mackinac. They are a very effective barrier to pollen and seed migration and have allowed the populations immediately to the north and to the south to develop differently in spite of essentially similar selection pressures. Conversely, free gene interchange has caused jack pine subpopulations several hundred miles apart in Minnesota and Wisconsin to develop similarly in spite of large differences in selection pressure.

Ecotypic organization of the species.—From differences in height when grown in Lower Michigan, Lake States jack pine can be regarded as comprised of four different ecotypes. This division is neither supported nor refuted by the data on insect attack because of the low statistical precision of those data. The proposed subdivision is as follows:

Ecotype	*Region of Origin*	*Remarks*
A	Western part of Michigan's Lower Peninsula	Significantly faster growing than ecotypes B, C, or D.
B	Eastern part of Michigan's Lower Peninsula	Significantly slower growing than ecotype A and significantly faster growing than most of ecotype D and all of ecotype C.
C	Michigan's Upper Peninsula	Significantly slower growing than ecotypes A or B and most of ecotype D.
D	Minnesota and Wisconsin	Intermediate between ecotypes B and C. More variable than other ecotypes in present tests.

Stoeckeler and Rudolf (1956) considered that their fall coloration data on these same jack pine provenances followed a clinal variation pattern, the southern provenances coloring later than the northern ones.[4] To determine whether this is the case, we grouped their data by ecotypes and by latitudinal belts (Tab. VIII). A comparison between these two methods of grouping indicate that the fall color data conform at least as well to the ecotypic as to the clinal variation pat-

[4] Their conclusion that the variation was continuous, varying directly with increasing latitude, was based on a correlation analysis. It is possible to obtain a significant correlation coefficient whether the variation is continuous or discontinuous. Analysis of variance is the proper test for discontinuities.

TABLE VIII

THE RELATIVE VALUE OF GROUPING BY GEOGRAPHIC ECOTYPES AND BY LATITUDINAL BELTS*
(IN PER CENT)

Region or Belt of Origin†	Range of Provenance Means from Stoeckeler and Rudolf's		
	Fig. 2‡	Fig. 3	Fig. 5
Comparison by ecotypes			
A	0–5	15–30	5–40
B	5–10	5–25	10
C	65–85	70–90	20–70
D	0–95	40–100	10–85
Comparison by latitudinal belts			
45–46° N.	0–45	25–60	10–40
46–47° N.	25–85	40–100	20–75
47–48° N.	30–95	85–100	40–90

* Based upon Stoeckeler and Rudolf's (1956) data on per cent of jack pines having purple fall color.

† Regions are as follows: A = western Lower Michigan; B = eastern Lower Michigan; C = Upper Michigan; D = Minnesota and Wisconsin. D also includes one seed source from Upper Michigan just over the Wisconsin border.

‡ Figs. 2, 3, and 5 are illustrations in Stoeckeler and Rudolf's paper.

tern. As with the height data, ecotypes A, B, and C seem fairly uniform within themselves whereas D is variable.

Practical and theoretical implications.—The differences in height growth are of practical significance to tree planters, especially to those in Lower Michigan. Jack pine originating from seed collected in the western part of Lower Michigan grew faster in Lower Michigan itself than the seedlings from all other seed sources collected in the Lake States—especially those from the Upper Peninsula of Michigan.

On the other hand, how seedlings from seed collected in western Lower Michigan grow in other parts of the Lake States remains to be determined from outplantings in those areas. Perhaps they will do well anywhere within the range of this provenance study.

Insofar as can be determined by the present analysis, the ecotypes from Regions A, B, and C are essentially homogenous to date except in resistance to bark beetle attack. This does not mean that no genetic

improvement can be expected as the result of individual selection and breeding studies within one of those regions. The precision of this study was such that only differences between provenances equal to 5 or 6 per cent of the mean were detectable. Smaller differences could be detected in other tests which had a greater number of replications.

Also, all the seed origins used in this experiment consisted of seed collected from a number of parent trees. Therefore, the test gave no measure of the magnitude of the individual-tree variation, which may be considerable. As a matter of fact, T. D. Rudolph et al. (1959) have already demonstrated the presence of considerable such variation in earliness of cone opening.

The differences in resistance to sawfly and bark beetle are only of theoretical interest at the present time. Not only are the differences small but the really outstanding provenances are undesirable because they are more rather than less susceptible than the average. The fact that genetic differences were demonstrated in these characters, however, indicates the possibility of improvement by genetic means.

Prior to these 5-year results very little precise information has been available on the applicability of the results of one provenance test to conditions in other localities. The similarity of results among the three Lower Michigan outplantings indicates that the results of one series of tests can be used to guide planting operations on similar sites over an area of at least a few thousand square miles.

Summary

In the autumn of 1951 seeds were collected from average jack pine stands in 29 localities of Michigan, Wisconsin, and Minnesota. They were sown in a Wisconsin nursery in the spring of 1952, and the resulting seedlings were grown there for 2 years. This study reports the first 5-year results from 2-0 seedlings outplanted at three locations in the northern part of Lower Michigan in the spring of 1954. At each location the test planting consisted of a 4-replicate, 64-tree-per-plot randomized complete block design; the trees were planted 6 feet apart in furrows.

The 5-year-old (from planting) test plantations were measured in the fall of 1958. These measurements and enumeration data were subjected to variance, multiple-range, or binomial analysis.

Two seed origins from the western part of Michigan's Lower

Peninsula grew significantly faster than any others included in the test. Next were two provenances from the eastern part of Lower Michigan, then several from Wisconsin and Minnesota, and last, four provenances from Upper Michigan. The Upper Michigan trees were about 20 per cent shorter than those in Lower Michigan. Significant differences among provenances were also found in susceptibility to bark beetles, white-pine weevil, and sawfly, but not in earliness of cone production, resistance to other pests, or oak-pine gall rust.

The variation in height growth of Lake States jack pine when grown in Lower Michigan is best described as ecotypic. The Lake States population seems to consist of three more or less distinct ecotypes (A and B from the western and eastern parts of Lower Michigan and C from Upper Michigan) and one variable ecotype (D from Wisconsin and Minnesota). Because quantitative data can be subjected to more precise statistical analysis than enumeration data, the height data were used for the delimitation of the ecotypes. However, the delimitation also fits the weevil and sawfly, as well as fall color data reported earlier by Stoeckeler and Rudolf.

All the provenances had the same (within the limits of experimental error) performance ratings at each of the three sites, indicating that the information gained from these plantings is applicable over a wide area in Lower Michigan.

LITERATURE CITED

Duncan, David B. 1955. Multiple Range and Multiple *F* Tests. Biometrics, 11:1–42.

Rudolf, Paul O. 1958. Silvical Characteristics of Jack Pine (*Pinus banksiana*). U. S. Forest Serv., Lake States Forest Expt. Sta., Sta. Paper 61, 31 pp., illus.

Rudolph, T. D., R. E. Schoenike, and T. Schantz-Hansen. 1959. Results of One-Parent Progeny Tests Relating to the Inheritance of Open and Closed Cones in Jack Pine. Univ. Minn. Forestry Note 78, 2 pp.

Schantz-Hansen, T., and R. A. Jensen. 1952. The Effect of Source of Seed on Growth of Jack Pine. Journ. Forestry, 50:539–544, illus.

—— and ——. 1954. A Study of Jack Pine Source of Seed. Univ. Minn. Forestry Note 25, 2 pp.

Schoenike, R. E., T. D. Rudolph, and T. Schantz-Hansen. 1959. Cone Characteristics in a Jack Pine Seed Source Plantation. Univ. Minn. Forestry Note 76, 2 pp.

Stoeckeler, J. H., and P. O. Rudolf. 1956. Winter Coloration and Growth of Jack Pine in the Nursery as Affected by Seed Source. Ztschr. Forstgenetik u. Forstpflanzenzüchtung, 5:161–165, illus.

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TEMPERATURES NEAR THE GROUND DURING PRESCRIBED BURNING

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Forest fires inherently do not lend themselves to quantitative description. The difficulty in measuring something as large and as dynamic as a moving forest fire has to date relegated descriptions of fire intensity to ambiguous and noncomparative terms such as "hot," "very hot," or "cool burning." Before any real analysis of fire behavior and fire effects can be made, absolute measures of fire intensity in terms of rate of heat release and temperature reached will have to be developed.

Actual measurement of fire intensity or the B.T.U.'s released per foot of fire front per unit of time (Byram, 1959) would require simultaneous measurement of many parameters. This would be a time-consuming undertaking, necessitating a lot of expensive equipment. Determination of a fire's thermal behavior would not be nearly so difficult and would in itself be a good description of a fire's behavior. Temperatures reached internally by a fire are a function of the rate at which heat energy is released by a fire, minus the rate at which this heat energy is lost to the environment. Temperature behavior of several moving fires was recorded for this preliminary study. Thermocouples were located at fixed points, temperature being recorded periodically as the fire moved through these points.

Procedure

Test fires were conducted in two widely separated fuels. One fire was burned in jack pine slash near Grayling, Michigan, in conjunction with William R. Beaufait and the Michigan Department of Conservation. Several fires were burned in the palmetto-gallberry fuels found in the Lower Coastal Plain of Georgia. This burning was in the course of investigations carried on by the Southern Forest Fire Laboratory of the U.S. Forest Service.

The Michigan fire was burned in the late spring of 1959. Fuel consisted of heavy, well-distributed jack pine slash left by a logging

operation the previous fall. Approximately 7 acres were burned, with the fire heading through all temperature measuring points.

The several Georgia fires were burned in the summer of 1959. Fuels burned varied considerably, in both quantity and composition. Palmetto was more predominant in some plots, gallberry in others. A loose pine needle mat of varying thickness was present on all plots.

Procedure followed in measuring temperatures was slightly different for the two burning locations. For the Michigan fires, chromel-alumel thermocouples were used, and temperatures were recorded on potentiometers. These have the advantage that they draw no current when balanced and that the thermoelectric e.m.f. can be read directly. Manually balanced potentiometers are slow to use, however; and temperatures cannot be read at close time intervals. Temperature measurements were taken for 4″, 1′, and 4′ heights aboveground.

Iron-constantan thermocouples were connected to galvanometers (milliammeters) to record temperatures for the Georgia burns. These instruments can be read continuously but draw current and have to be calibrated in the laboratory to convert the readings to actual temperatures. Thermocouples were located at 1′ and 4′ heights aboveground for the Georgia burns.

Reference junctions and lead cables were buried at least 6 inches underground in both the Michigan and the Georgia burns. Recent testing of thermocouples with high temperature silica glass insulation protected with a stainless steel armor has shown that it is possible to string the lead wires aboveground. This considerably reduces the time required to set up the equipment in the field.

Data and Discussion

Each series of temperature readings, taken for each thermocouple location, are plotted graphically, using time as the abscissa. Three sets of temperature curves for the Michigan headfire and one set for each of the 3 headfires and 2 backfires in Georgia are presented in this paper. Uncalibrated temperature data for 6 other Georgia fires, although not here included, have been used in arriving at some of the more general relationships.

Figs. 1, 2, and 3 are time temperature curves of headfires in jack pine slash. Figs. 4, 5, and 6 are time temperature curves of headfires in palmetto-gallberry fuels; and Figs. 7 and 8 are of backfires in these same fuels. The difference in time scales between jack pine fires and

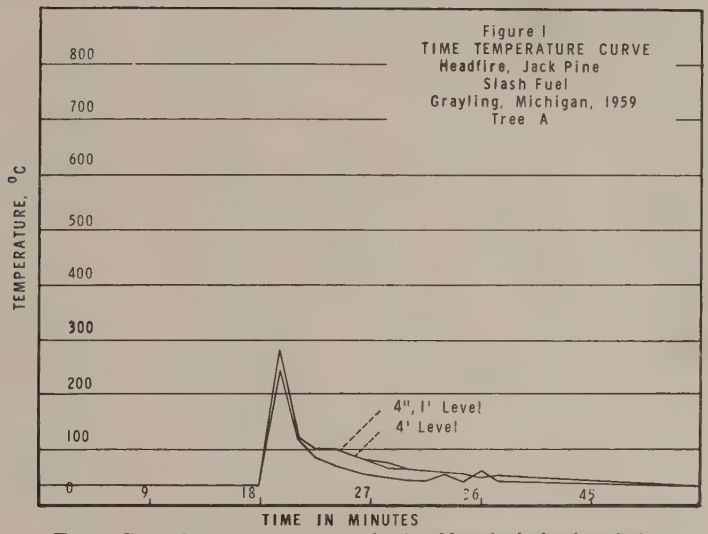


FIG. 1. General temperature curve for headfires in jack pine slash.

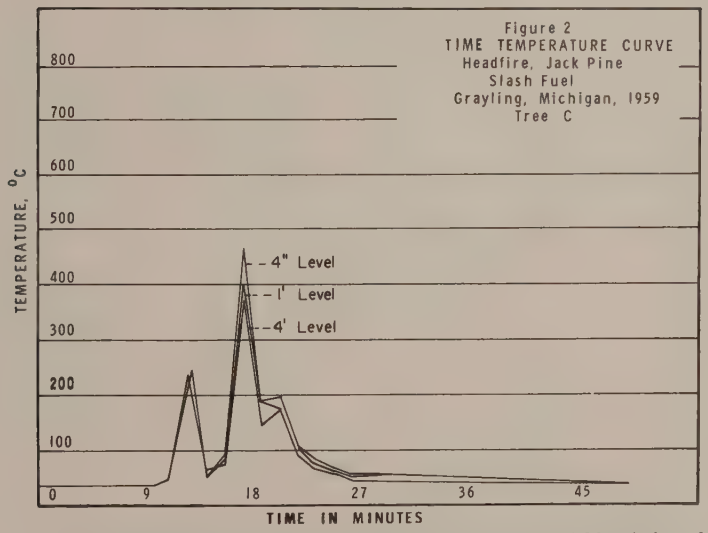


FIG. 2. Double peaking of the temperature curve is caused by variable winds and an irregular fire front. Temperatures decrease with height—the normal temperature profile.

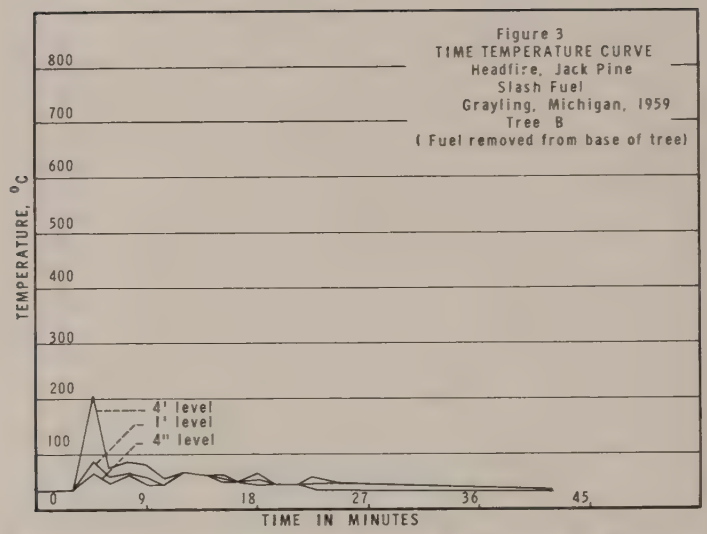


FIG. 3. Inversion of the normal temperature profile illustrates the effect of removing fuels below the measuring points.

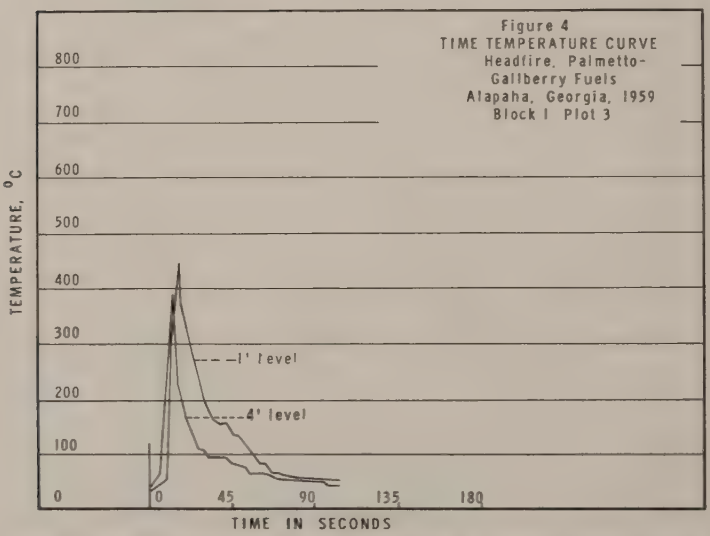


FIG. 4. General temperature curve for headfires in palmetto-gallberry fuels.

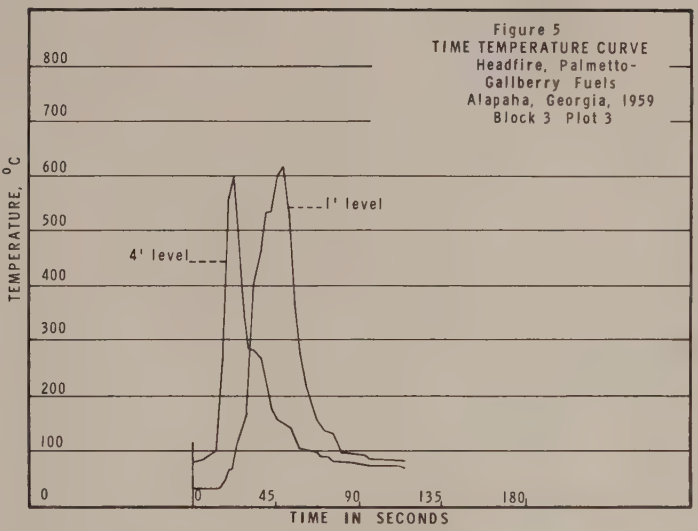


FIG. 5. The wind inclines the flames and convection currents, causing earlier peaking at the higher measurement points than at the lower.

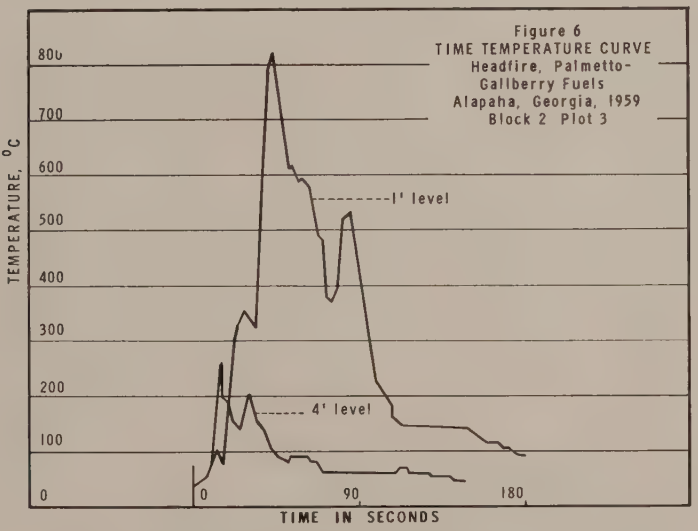
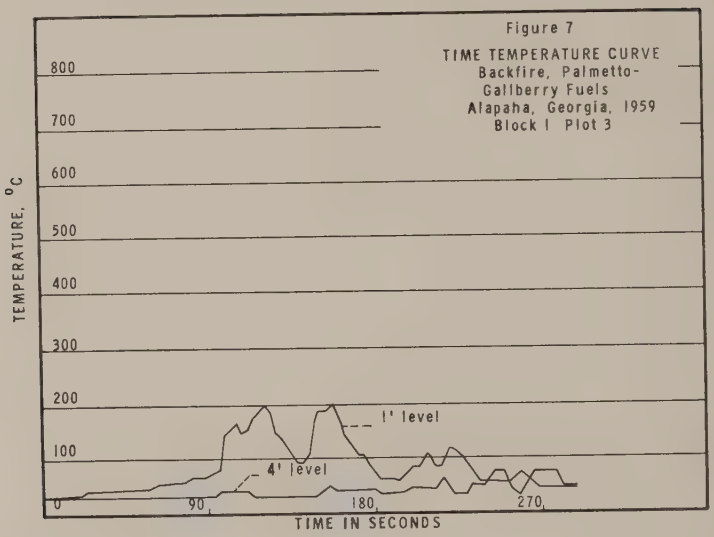
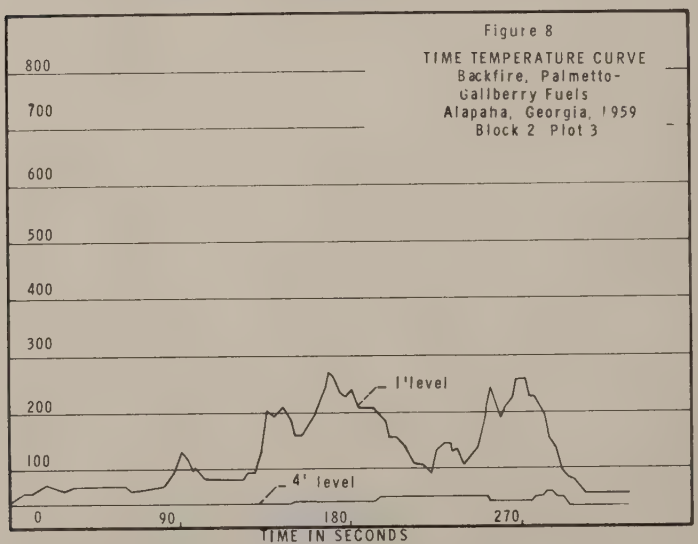


FIG. 6. Normal temperature profile with temperatures dropping rapidly with height.





FIGS. 7 and 8. Temperatures recorded in backfires are much lower than those in headfires. Negligible heating occurs at the 4-foot level.

palmetto-gallberry fires should be noted. Vertical temperature scales are the same for both fuels. Due to the long time intervals used in reading the temperatures for the jack pine fires, it is almost certain that the peak temperatures were not recorded. The overall curve shape should be correct, however.

Fire behavior is difficult to pin down; nevertheless, the limited data already obtained does permit several general conclusions to be drawn. First, it can readily be seen that the time temperature curves for headfires and backfires are distinctly different. Headfire temperatures will rise rapidly to a peak and, as the fire front passes, drop rapidly at first and then at a decreasing rate. Backfires characteristically exhibit a slow temperature rise, peak at much lower temperatures than headfires, and maintain this peak for a longer time before the temperature begins to fall off.

This behavior would be in accordance with the results of Fons (1950) who studied the rates of ignition of wooden sticks ranging from ⅛″ to ⅜″ in diameter. He found that above 1300° F. (704° C.) all sizes of sticks ignited at about the same time. As temperatures were lowered below 1300°, the ignition time for all sticks increased, the increase being greater for the larger sticks.

Keeping this in mind, we will now look at a fire as a dynamic system, a system that reaches an equilibrium for each fuel and burning condition. A fast-moving headfire, moving before the wind, builds to an equilibrium condition of high fuel consumption rates. The backfire, moving slowly into the wind, reaches an equilibrium at much lower rates of fuel consumption. The rapid burning of headfires produces high rates of heat yield and high temperatures, permitting a wide range in sizes of fuels to be ignited simultaneously. This, in turn, sustains the high temperatures and rates of heat yield. Backfires, by the same reasoning, have low rates of heat yield and low temperatures. Ignition would progress from the finer to the coarser fuels. The lower rate of ignition and burning produces lower temperatures and heat yields, bringing the system to an equilibrium at a lower level than for headfires.

The rate of temperature decline after peaking is much lower in the Michigan fire than in the Georgia burns, as shown in Fig. 9. This may be explained by the heterogeneous composition of forest fuels. In the Georgia fires, mostly fine fuels were burned; in the Michigan fire, the fuels consumed ranged in size from needles, leaves, and grasses to stems of an inch in diameter. The sharp peaking of the

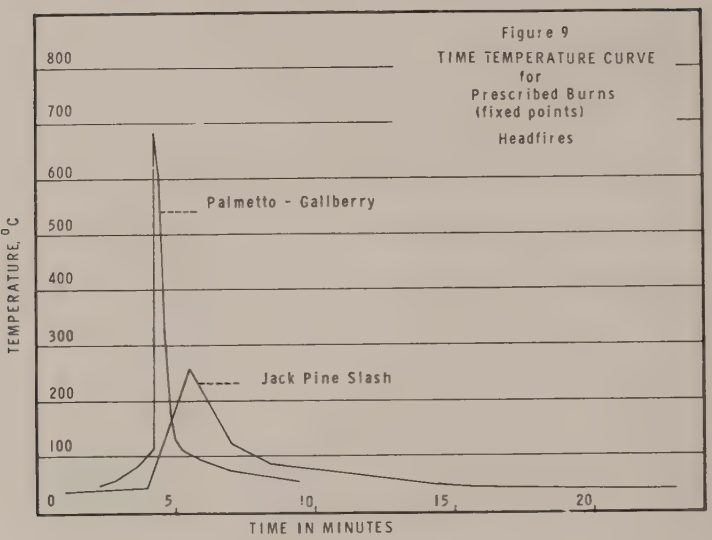


FIG. 9. Recorded temperatures were lower but the breadths of the curves greater in jack pine slash fuels than in palmetto-gallberry fuels. Peak temperatures were undoubtedly not recorded in the jack pine slash fires.

headfire temperature curve occurs when the fuels are first ignited at the point of measurement and the flames reach their greatest heights. If only the finer fuels are burned, as in the Georgia fires, the fire will die out rapidly and will be indicated by a rapid decline in the temperature curve. When the coarser fuels, such as stems and dead branches, are ignited and continue burning, heat will continue to be released and the temperature curve will decline slowly. This was the behavior displayed by the Michigan fire.

Temperature declines rapidly with height aboveground, the decline starting somewhere within the flame zone of the fire. From our limited observation, the rate of temperature decline with height appears to be either exponential or hyperbolic. This relationship generally holds true for both head and back fires and for all points along the time temperature curves. The temperature decline is undoubtedly due to a combination of radiation loss and entrainment of air in the

thermal column. From visual observation of crown damage, the rate of temperature decline with height is increased when a headfire burns in a light breeze rather than in a still atmosphere.

The temperature curve at the 4-foot level peaks earlier than the curve at the 1-foot level for a headfire, whereas the reverse is true for a backfire. This is to be expected, as the wind will incline the flames and convection currents, causing the higher levels to be heated first.

Applications

Description of a forest fire in terms of its characteristic time temperature curve will have valuable applications in practical forest fire research, use, and control. If a forester wished to prescribe fire to accomplish a specific objective in a forest stand, he could well afford to consider the time temperature curves which might result from the fire. To stimulate seed dissemination from serotinous cones, a fire would be needed that would develop sufficiently high temperatures in the tree crowns. In most cases, a headfire would be preferable since backfires seldom develop the temperatures needed. If the tree crowns are low and there is a danger of the fire jumping into them, a backfire might be more desirable, as flame heights are lower. Backfires might be more useful when burning for seedbed preparation. The slower rate of spread and longer temperature duration facilitate the drying of moist litter and duff, thus causing the fire to burn closer to mineral soil.

Fuels could be evaluated in terms of the time temperature curves exhibited by test fires burned through them. This approach would clearly indicate what fire intensities and damage could be expected from wildfires burning in these same fuels.

In the extreme case of fire behavior, that of the "blowup" fire, the contribution of the fuel to the blowup condition might be ascertained. The time temperature curve would be not only an indication of the heat energy available from the fire to cause the blowup, but also what fraction of the fuel contributed to it.

Further time temperature relationships of fires may have wide application in the use of fire to selectively remove some vegetation from a forest stand. Vegetative damage has been shown to be a function of the temperature to which living tissue is raised and also the duration at that temperature (Collander, 1924; Fons, 1950; Nelson, 1952;

Shirley, 1936). No conclusive differences in the lethal time temperature factor have been observed between species of higher plants. An important difference does exist, however, in the insulation afforded by bark to the different species and to different ages of each species. By properly selecting the burning conditions and type of fire, it would be possible to remove more poorly insulated trees, while sparing the better insulated ones. Thin-barked hardwood species competing with the thick-barked and more valuable pines could be removed in this manner. Trees small in diameter could easily be removed from a stand, leaving only those of larger diameter.

A mathematical fit as an expression of the time temperature curve would facilitate their application. With such a mathematical expression, it would be possible to describe a fire's behavior in terms of two or more parameters or parameter ratios. These parameters might be basic factors affecting fire, combinations of basic factors, or merely empirical constants.

This mathematical expression could be used immediately as the heat source input, using an analog computer, in determining heat flow in trees during fires. We have made preliminary mathematical fits; but we have not been too successful owing to the great variation in burning conditions. A series of burns now being conducted at the Southern Forest Fire Laboratory should provide sufficient control of fuels and burning conditions to yield a useful mathematical expression.

Continued research will be necessary to more accurately quantify the time temperature relationships of forest fires. Better controls will be needed on both fuels and burning conditions. Laboratory studies will be needed to provide more basic data on combustion of forest fuels and to provide models simulating behavior of forest fires. From these studies should come a better understanding of forest fire phenomena with the attendant application of the new knowledge to improve our use and control of fire.

BIBLIOGRAPHY

Baker, F. S., 1929. The Effect of Excessively High Temperatures on Coniferous Reproduction. Jour. Forestry, 27:949–975.

Byram, G. M., 1959. Chapter III *in* Davis, K. P., Forest Fire Control and Use. 1959, 3: 77–79.

Collander, R., 1924. Beobachtungen über die quantitaven Beziehungen zwischen

Fösungsgeschwindigkeit und Temperatur beim Warmentod pflanzlicher zellen. Finska vetenskaps-societeten (Soc. Sci. Fennica) Com-Biol. 1 no. 7: 1–12.

Fons, W. L., 1950. Heating and Ignition of Small Wood Cylinders. Ind. and Engin. Chem., 42: 2130–2133.

Nelson, R. M., 1952. Observations on Heat Tolerance of Southern Pine Needles. U. S. Forest Serv. Southeast. Forest Expt. Sta. Paper 14.

Shirley, H. L., 1936. Lethal High Temperatures for Conifers and the Cooling Effect of Transpiration. Jour. Agr. Res., 53: 239–258.

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CROWN TEMPERATURES DURING PRESCRIBED BURNING IN JACK PINE

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Prescribed fire, already accepted as a useful silvicultural tool in the South, has recently been under study in Canada and the Lake States for its application in the regeneration of jack pine, *Pinus banksiana* Lamb. (Beaufait, 1959; Chrosciewicz, 1959). Advantages of prescribed burning in this type include preparation of a mineral seedbed and exposure of serotinous cones to temperatures likely to assist dispersal of seeds.

The serotinous or closed-cone habit of jack pine has long been a problem to foresters seeking natural regeneration in merchantable and mature stands. Viable seeds may remain locked in serotinous cones for up to 25 years (Ellis, 1911). Temperatures in excess of 140° F. must be reached to melt the resin which bonds cone scales together (Cameron, 1953). Because such high temperatures do not normally occur in the crowns of cone-bearing trees, large quantities of seeds accumulate in maturing stands. Eyre (1938) estimated that serotinous cones in well-stocked stands of jack pine in Minnesota could contain an average of 2,000,000 seeds per acre.

This regeneration potential has been tapped in the past by wild crown fires in standing timber and by uncontrolled slash burns after the logging of virgin stands. Nearly all of our present stands of jack pine originate from an otherwise devastating fire. Unfortunately, wild fires do not always occur when conditions are favorable for seed germination or seedling survival. As a result, many acres of forest land lie unproductive today.

Since 1957, the Department of Conservation has conducted 6 prescribed fires in harvested stands of jack pine in northern Lower Michigan. The author is now continuing his work at the Ford Forestry Center by scheduling 2 more for this coming season in the Upper Peninsula. All past burns were in the late spring. This year we shall have our first autumn fire.

As a rule, 15 to 20 evenly distributed seed trees per acre are

marked to leave before cutting operations begin. Slash from the harvested trees provides a relatively uniform fuel supply after a curing period of 1 to 4 months. Slash depth ranges between 18 and 30 inches. Every effort should be made to have the fuel as evenly distributed as possible.

Results of past burns have been consistently positive (Beaufait, 1959). Significant variation exists, however, in the number of seedlings established after prescribed burns. While most of this variability is a function of weather conditions after the fire, some is due to differing availability of seeds from the cones of seed trees. This indicates that crown temperatures during the fire may be of critical importance.

Since the melting point of cone resin is 140° F., the question arises concerning the time required at temperatures above 140° F. for melting of the resin bond and initiation of the physical processes involved in cone opening. As part of a separate study of cone scale structure and the effects of high temperatures on cones (Beaufait, 1960) it has been determined that the intervals between cone opening and ignition lie in a range of temperatures between 200° F. and 1300° F. These data are presented in Fig. 1. Moreover, it was found that cone ignition

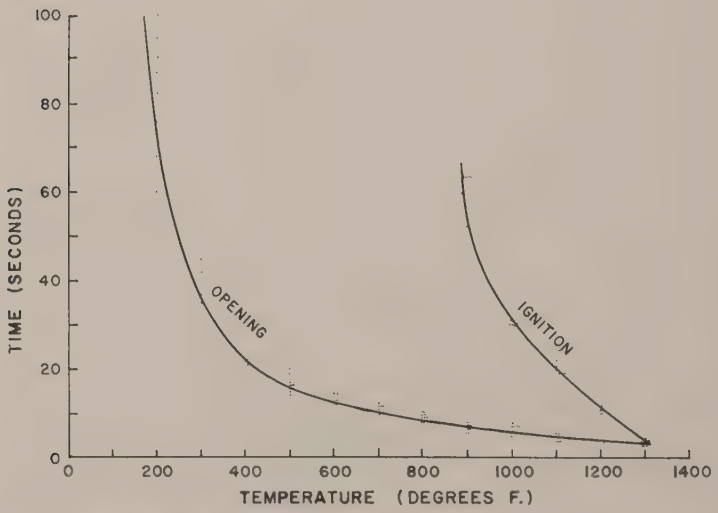

FIG. 1. Cone opening and ignition curves for cones at 8 per cent moisture content (O.D.W. basis) in an open muffle furnace.

is accompanied by complete loss of seed viability. This, incidently, supports Eyre's (1938) observation that cones and the seeds contained within are destroyed in burning slash.

What then are the temperatures and durations that occur in the crowns of seed tree crowns during a prescribed fire? Initial work to establish critical temperatures was necessarily rather empirical. Lacquers which fuse at temperatures from 113° F. to 1500° F. were painted on asbestos boards attached to metal pipes. These pipes were erected within the areas to be burned and the boards were inclined on them at a 45° angle. Maximum temperatures were recorded at 1, 5, 9, 13, and 17 feet above the ground at 6 locations in each of two burns. Temperature maxima varied, depending upon slash density, from 1400° F., at 1 foot above the ground, to an average of 600° F. at 17 feet. Burning index seemed to exert an influence on temperatures reached at higher elevations. All cones in the seed trees opened during these two fires.

In the spring of 1959, a 10-acre prescribed fire was conducted near Grayling, Michigan. In this experiment, four typical seed trees were selected for more complete instrumentation than had hitherto been used. Unshielded iron-constantin thermocouples were placed at 10-, 25-, and 50-foot elevations in the crown of each tree. Protected by asbestos paper on the lower boles, the wires were led to a cold junction buried at the base of each tree, thence underground, where copper wire carried the current outside the burned area to a portable potentiometer. A switch box enabled the operator to read temperatures sequentially at all 12 thermocouples. Fig. 2 illustrates the apparatus in use during the actual fire.

The burning index on the afternoon of this most recent fire was 16. Wind velocity ranged from 15 to 20 miles per hour. For the first time we were unable to achieve 100 per cent cone opening. However, this provided some comparison of temperatures where cones did or did not open.

Fig. 3 presents time-temperature records for one of the sample seed trees. The data begin with 100° F., since instrumentation at lower temperatures was not practicable on this occasion. It must be recognized, however, that temperatures below 100° F. contribute to the heating of cones. Because thermocouple temperatures were read every 20 to 30 seconds, many of the rapid fluctuations could not be recorded. Also, because bare thermocouples were used, the radiant energy intercepted may not always be fully representative of ambient air tem-

FIG. 2. Portable potentiometers in use on a prescribed slash fire. Thermocouples are installed on seed trees about 200 feet within the fire.

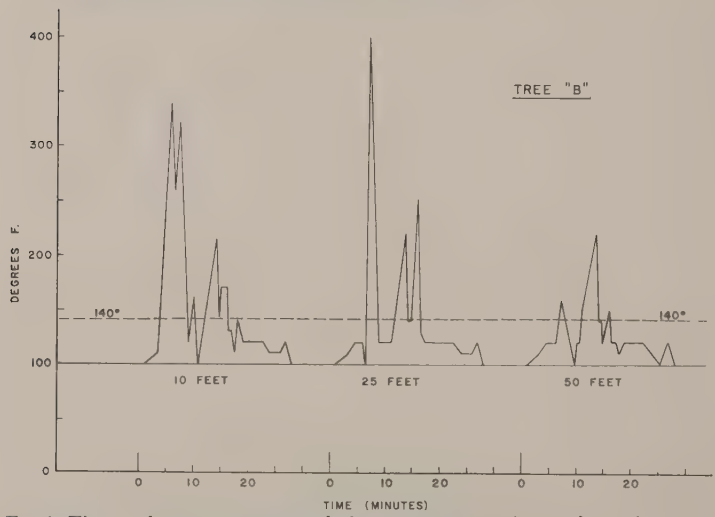

FIG. 3. Time and temperature records from a representative seed tree in a prescribed slash fire. Thermocouples are located 10, 25, and 50 feet above the ground.

peratures. Owing to the small diameter of the couples (B and S gauge No. 30), however, the data obtained may be considered quite adequate and representative. Since heat transmission through cone scales is not well understood and many variables influence the kinds of heat transfer in forest fires (i.e., radiation, convection, and conduction), it is not yet possible fully to evaluate the heat gain and loss expressed by these curves. These values can, however, be integrated for presentation as cumulative gain, as in Fig. 4.

At the 50-foot level, the total number of degree-minutes above 0° F. is 3,215, at the 25-foot level, 3,815, and at the 10-foot elevation, 4,141, all occurring over a period of 27 minutes. While the differences do not appear to be great, cones were opened at 10 and 25 feet, but not at 50 feet. Because of the unknown heat factors mentioned above, however, we cannot yet conclude that cone opening requires between 3,200 and 3,800 degree-minutes exposure. Indeed, Fig. 1 has shown that only 82 to 263 degree-minutes are needed to open cones exposed to constant temperatures. The great disparity between these figures and those obtained during the prescribed fire may be ascribed to temperature fluctuations during the burn. Future work will be directed toward explanation of these differences.

The preliminary work described above has served to define a problem. As prescribed fire finds greater and greater applicability in the Lake States, practicing foresters will need criteria for judging the appropriate times for ignition. Information on fuel and weather conditions required for successful burns must come from more fully instrumented experiments.

Since the cost and intensive preparations required on many experimental fires can easily become prohibitive, empirical determination of fire behavior under all levels of slash moisture content and weather conditions cannot be made. It is therefore necessary to resort to mathematical models on theoretical burns to fill the gap between conditions actually measured and the range of possible fuel and weather variables that may be encountered in nature.

One alternative approach concerns the determination of heat output by measured quantities of slash fuel of different moisture contents. Sampling of fuel mass in representative cut-over stands will be required to establish practicable limits. Since slash is normally composed of all sizes of material from needles to large limbs and tops, the proportions of each must be determined.

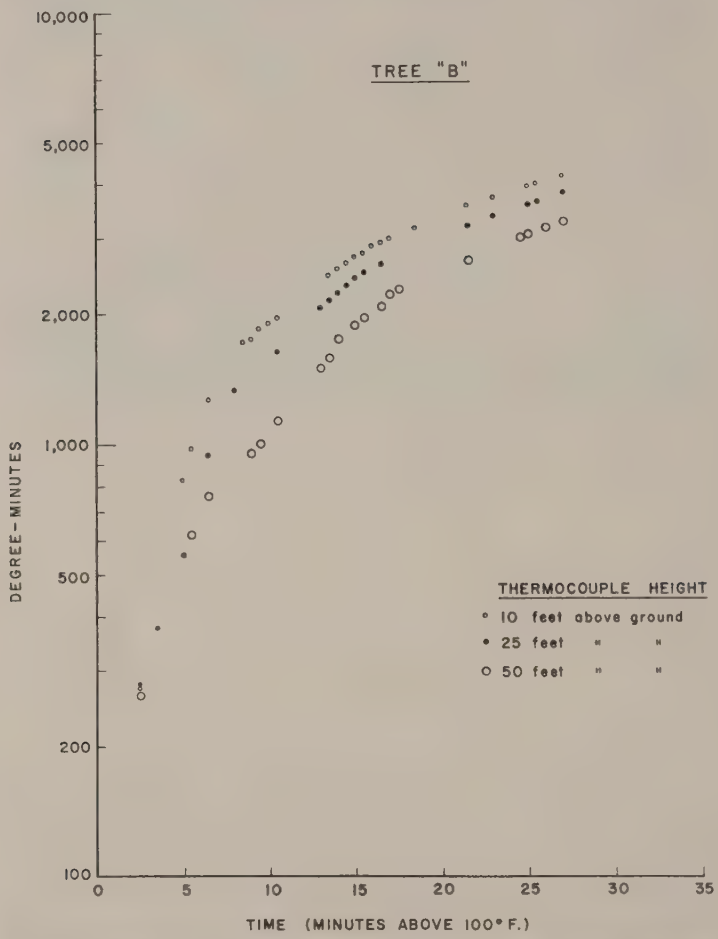

FIG. 4. Cumulative time-temperature curves from the three tracings illustrated in Fig. 3.

We are then faced with the necessity of finding a practical way for the forester to measure fuel moisture content. Fortunately, standardized basswood or white pine slats, available at most fire danger stations, can be calibrated and installed on proposed burn sites prior to

the fires. Regular measurements will then indicate when fuel conditions are optimal.

Still another approach to the problem will involve model fires. This year small scale slash burns will be conducted at the Ford Forestry Center by transporting fuel to a completely instrumented 1/40th acre plot. Multiple-point potentiometric recorders will permit evaluation of the relative influence of the three heat transfer phenomena that act differentially at different heights above the fire. The forest burns already planned will also make use of continuous recordings to provide data on larger-scale fires. In this way, measurements made during small tests can be adjusted for gross influences normally found in the field.

We have seen how jack pine cones open at different rates depending upon the level of temperature exposure. Laboratory determination of the number of degree-minutes required for cone opening can only be used as guides in the evaluation of how cones are affected during prescribed fires. As data accumulate from both large and small scale burns, foresters will be able to predict the efficiency of proposed fires in accomplishing silvicultural tasks. When properly employed, prescribed fire can be fully justified as an economic expedient in site preparation and cone-opening. Other applications will doubtless develop as increasing demands upon our forest resource dictate more intensive management practices.

BIBLIOGRAPHY

Beaufait, W. R. 1959. Studies of Fire and Other Factors Related to Jack Pine Regeneration in Northern Lower Michigan. Ph.D dissertation. University of Michigan, ix + 170 pp.

——. 1960. Some Effects of High Temperatures on Cones and Seeds of Jack Pine. For. Sci. (In press).

Cameron, H. 1953. Melting Point of the Bonding Material in Lodgepole Pine and Jack Pine Cones. Canada Dept. Resources and Development, Forestry Branch, Silv. Leafl. No. 86. 3 pp.

Chrosciewicz, Z. 1959. Controlled Burning Experiments on Jack Pine Sites. Canada Dept. Northern Affairs and National Resources, Forestry Branch, Tech. Note No. 72. 19 pp.

Ellis, L. M. 1911. Some Notes on Jack Pine (*Pinus divaricata*) in Western Ontario. For. Quart. 9: 1–14.

Eyre, F. H. 1938. Can Jack Pine Be Regenerated without Fire? J. For., 36: 1067–1072.

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SOME OBSERVATIONS ON A VIRGIN STAND OF EASTERN WHITE PINE

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It seems safe to conclude that a naturally occurring, mature forest stand in a given locality represents a reasonable approximation of what that locality, or similar areas elsewhere, could reproduce under equivalent conditions. Similarly, the actual composition of an existing natural stand is the fairest expression of the kind of forest which probably characterized all these places, regardless of subsequent drastic changes which may have occurred. This paper is concerned with observations on the last large stand of old-growth "sand plains" eastern white pine in Baraga County, Michigan. The tract was a remnant of an even larger acreage once found on dissected glacial lake benches and other sandy sites peripheral to the Baraga Plains. Although the following observations were made in 1953, they now seem particularly pertinent as an indication of what hundreds of acres of young pine growth in the vicinity are capable of producing. Thus, they may serve as standards by which the success of present or future management of these stands can be evaluated.

It is unfortunate that study of "virgin" forests tends to lag when the acreage available is large, only to become active after stands have virtually disappeared. The present paper is a case in point, since the work was delayed until only a few days remained before commercial clear-cutting operations felled the last tree.

The stand in question was situated entirely in the NW 1/4 Sec. 6, T49N-R33W, Baraga County. Between 1936 and 1940, heavy partial cuttings had been made in the pine forest of contiguous sections; and by 1951, cutting had begun in Section 6. A U. S. Geological Survey aerial photograph made in October 1951 shows only about 70 acres remaining (Fig. 1), while by September 1953 logging of the entire tract was complete. Only about 20 acres remained, and active logging was in progress when the present measurements were made.

The terrain of the area is generally level to rolling. Pitting also occurs, the larger depressions being occupied by the Jackson Lakes.

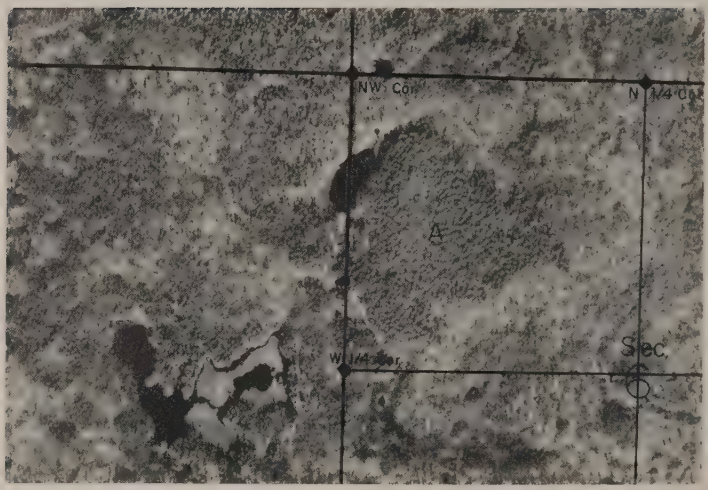

FIG. 1. Area occupied by old-growth eastern white pine stand in the NW ¼ Sec. 6, T49N-R33W, Baraga County, Michigan (from U. S. Geological Survey aerial photograph made in October, 1951). The stand is situated at "A."

The podzol soil has tentatively been classified as Vilas Sand, intergrading to Au Train Sand (because of intermittent induration in the B horizon). The pH of the various horizons ranges from 5.0 to 6.0.

A 2.4-acre sample of standing trees was obtained by systematically spacing twelve 1/5-acre circular plots in the uncut area. The diameter at breast height of every tree larger than 1 inch was recorded for each plot. A simple yoke served to measure trees smaller than 4 inches; a diameter tape was used in measuring the rest. Merchantable height was estimated on standing trees of all species except the pines. When felling and bucking into logs was completed, merchantable height for white pine was determined by 2-inch diameter classes on a 70-tree sample. This was accomplished by totaling the length of all logs actually sawed from each tree (Fig. 2). Total height was not taken because of the breakage tops sustained in felling. A 12-tree sample of red pine indicated that merchantable heights for both pine species were similar. Gross board foot volumes were computed by using the height data in conjunction with measured tree diameters. Subsequently, the same height data have been used in determining the vol-

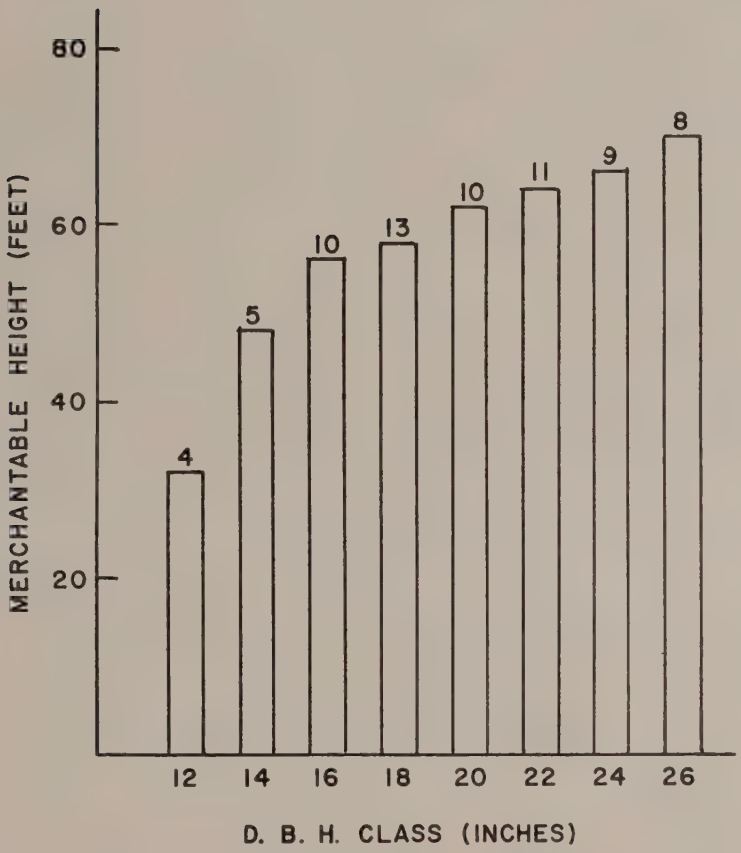

Fig. 2. The relationship of diameter breast height to actual merchantable height in an old-growth stand of eastern white pine, Baraga County, Michigan.

ume of standing trees in nearby areas. Virtually no "red heart" or other defect was present in the trees examined; therefore, net volumes did not differ materially from gross volumes.

It is understandable that early logging in Michigan was concentrated in the better pine areas. Frothingham (1914) writes that,

in the Lake States, "entire 'fortys' often averaged 50,000 feet per acre." He adds that townships were known to have "an average of about 18,000 feet per acre." Such stands appear to be similar in volume to the large remnants Chaffee (1924) studied in Pennsylvania. Timber such as this has virtually been eliminated from the Lower Peninsula of Michigan, while good stands in the Upper Peninsula have been decimated. The 1936 Forest Survey (Cunningham and White, 1941) found average volumes of old-growth white pine and red pine stands to be only 8,270 and 3,200 board feet per acre, respectively.

The tract in Baraga County certainly ranked among the better ones (Tab. I). Plot volumes ranged from 19,300 to 49,330 board feet per acre (International 1/4-inch rule), while the per acre average for the 12 plots was 36,022 board feet. It is interesting to note, also, that red pine volume amounted to 25 per cent of total volume, the same percentage published for red pine cut in Michigan during the 30-year period from 1880 to 1910 (Woolsey and Chapman, 1914).

TABLE I

Gross Board Foot Volume per Acre

Old-Growth Eastern White Pine Stand, Baraga County, Michigan

Species	Board Foot Volume per Acre (International ¼-inch Rule)*		
	Lowest plot	Highest plot	12-plot average†
White pine	17,525	26,330	25,499
Red pine	920	22,450	8,421
Hemlock	—	550	710
Balsam fir	—	—	33
Sugar maple	—	—	24
Red maple	855	—	494
Yellow birch	—	—	214
Paper birch	—	—	10
Balsam poplar	—	—	519
Red oak	—	—	98
Total	19,300	49,330	36,022

* Volumes are from the Lake States composite tables. No trees below the 12-inch diameter class are included.

† Circular ⅕-acre plots; 2.4 acres in the sample.

Of further interest are comparisons between the Baraga tract and the "Grayling Pine"—the present day Hartwick Pines, situated a few miles north of Grayling, Michigan. Wackerman (1924) gave the age of the latter as 166 years when he studied the stand. Annual ring counts on fresh stumps in the Baraga tract, on the other hand, averaged 141 years, with a maximum count of 147 years. Wackerman's reported stand volume of 34,000 board feet per acre for all species is only slightly less than that shown in Table I, although the "Grayling Pine" was several decades older.

Both stands appear to have had a similar history. Wackerman concluded that the stand he studied "was a long, rather narrow strip surrounded by old, mature pine and probably developed from reproduction after a storm . . ." Records of the General Land Office Survey provide the best evidence of the origin of the Baraga tract. The original township plat shows the area to lie in a "wind track," a term used by early surveyors to describe blowdowns resulting from heavy winds or tornadoes. Austin Burt's 1846 field notes list only aspen witness trees and line trees, and mention aspen alone as occurring in the vicinity. Apparently the pine was relatively small then and was developing under an aspen overstory. The size reported for aspen witness and line trees suggests that the blowdown must have occurred at least 20 or 30 years earlier.

According to Wackerman, the most recent 40-year gross increment in the Grayling stand was 292 board feet per acre per year. This is about 43 per cent greater than average net growth over the entire 166-year life of the stand. In comparison, net growth of the Baraga stand during its 141-year history averaged 255 board feet per acre per year. Basal area of the latter was 167 square feet in trees 12 inches and over (193 square feet in trees 2 inches and over), which supports field observation that overstocking had caused considerable slowing of current growth.

Tree diameters in the Baraga tract ranged from 6 to 34 inches for white pine and from 8 to 28 inches for red pine (Tab. II). Only a few large balsam poplars and paper birch remained of the presumed "nurse crop." A hardwood understory of 4- to 12-inch trees was well developed in places and consisted of red maple, yellow birch, and sugar maple, in that order of importance. An even denser growth consisting principally of balsam fir saplings appeared to constitute a third story. Hemlock was common and of the same general size as the hard-

TABLE II

TREE STAND PER ACRE

Old-Growth Eastern White Pine Stand, Baraga County, Michigan*

Diameter Class	Trees per Acre											
	White pine	Red pine	Hemlock	Balsam fir	White spruce	Sugar maple	Red maple	Yellow birch	Paper birch	Balsam poplar	Red oak	All species
2	—	—	—	380.0	—	6.6	20.0	13.3	—	—	—	419.9
4	—	—	1.2	9.6	0.4	2.1	1.7	1.2	—	—	—	16.2
6	0.4	—	6.2	9.2	1.2	1.7	4.6	4.2	—	—	—	27.5
8	3.3	0.8	8.7	—	0.4	2.5	7.9	5.0	—	—	—	28.6
10	3.3	0.4	2.9	—	1.7	1.2	4.6	1.7	0.4	—	—	16.2
12	2.9	0.8	5.4	0.4	—	0.4	6.2	0.8	0.4	—	—	17.3
14	1.7	1.2	2.5	—	—	—	1.2	0.8	—	—	—	7.4
16	5.4	0.4	0.8	—	—	—	—	0.4	0.4	0.4	0.4	8.2
18	7.1	2.1	—	—	—	—	—	—	—	0.8	—	10.0
20	7.5	3.8	—	—	—	—	—	—	—	—	—	11.3
22	5.0	4.6	—	—	—	—	—	—	—	—	—	9.6
24	4.6	1.2	—	—	—	—	—	—	—	0.4	—	6.2
26	4.2	1.2	—	—	—	—	—	—	—	—	—	5.4
28	3.3	0.4	—	—	—	—	—	—	—	—	—	3.7
30	0.8	—	—	—	—	—	—	—	—	—	—	0.8
32	0.4	—	—	—	—	—	—	—	—	—	—	0.4
34	0.8	—	—	—	—	—	—	—	—	—	—	0.8
Total	50.7	16.9	27.2	399.2	3.7	14.5	46.2	27.4	1.2	1.6	0.4	589.5

* Based on a 2.4 acre sample.

woods. However, the age of hemlocks representative of all size classes was roughly as great as that of the pines, indicating concurrent origin. It should be noted that practically no trees larger than 4 inches remain in the area today, except for a few spindly white pine. The rest either were removed by logging, destroyed by felling of the larger trees, or killed by subsequent exposure. Pioneer hardwoods again predominate, with some small white pine seedlings developing among them.

Unfortunately, Wackerman published no stand table for the "Grayling Pine," but stated that trees "range in diameter from 10 to 24 inches and in height from 90 to 125 feet, but old veterans have diameters up to 36 inches and heights up to 160 feet." A stand table based on an extremely small sample was published by Kittredge and Chittenden (1929) for the Interlochen, Michigan, "virgin" pine. It appears to represent a radically different kind of stand in which an abundance of white pine reproduction occurs among small hardwoods under an open overstory of 22 to 24 inch white pine veterans.

Data on the Baraga tract establish a growth potential for this and similar areas which should encourage continued management of them for the production of mixed white and red pine timber. Any of several management practices should certainly contribute to a much shorter rotation than 141 years. Intermediate harvests, coupled with other treatments designed to maintain optimum growth on crop trees, could result in average yields per acre even greater than those that observations on the natural stand have indicated as possible.

LITERATURE CITED

Chaffee, R. R. 1924. Comparison of the Volumes of Virgin White Pine Stands in Pennsylvania. J. For., 22: 190–192.

Cunningham, R. N., and White, H. G. 1941. Forest Resources of the Upper Peninsula of Michigan. U.S.D.A. Misc. Publ. No. 429. 32 pp.

Frothingham, E. H. 1914. White Pine under Forest Management. U.S.D.A. Bull. No. 13. 70 pp.

Gevorkiantz, S. R., and Zon, R. 1930. Second-Growth White Pine in Wisconsin. Univ. of Wisc. Agric. Exper. Sta. Res. Bull. No. 98. 40 pp.

Kittredge, J., and Chittenden, A. K. 1929. Oak Forests of Northern Michigan. Mich. State Coll. Agric. Exper. Sta. Spec. Bull. 190. 47 pp.

Wackerman, A. E. 1924. Growth of the "Grayling Pine." J. For., 22: 936–937.

Woolsey, T. S., and Chapman, H. H. 1914. Norway Pine in the Lake States. U.S.D.A. Bull. No. 139. 42 pp.

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THE EFFECTS OF STOCKING LEVEL CUTTINGS ON THE VOLUME AND VALUE OF RESIDUAL TIMBER IN A NORTHERN HARDWOOD STAND

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Forest stocking can be defined simply as stand density. It is a measure of what is actually on the land at a given time. Among the different measurements used to indicate stocking are stand volume, basal area, number and diameter distribution of trees, bole area, crown closure, and stand density index. Of these, basal area is one of the most widely used because it is easily determined and is independent of tree height.

Partial cuttings have been made in Lake States northern hardwoods for the past 30 years. Eyre and Zillgitt (1953) analyzed the effects of these partial cuts and found that a residual basal area of about 70 square feet, in trees 10 inches d.b.h. (diameter breast height), and larger, provided optimum conditions for regeneration and growth. Foresters now want additional information on the effects of residual stand density or stocking level. They need answers to the following questions: Does cutting to different stocking levels change the percentage of cull in the residual stand? If so, can net tree volume be determined with sufficient accuracy to detect such differences? How do stocking levels affect the volume and value of the timber removed? And how are residual volumes and values affected? Does the percentage of residual volume in various log grades change due to stocking level?

To shed some light on these questions, a study was conducted in Upper Michigan during the summer of 1959. This paper reports the results of that study.

Description of Study

Marking.—A 2½-acre stand of old-growth northern hardwoods, representative of much of the mature northern hardwoods in Upper

* The author gratefully acknowledges the assistance of Wilho H. Salminen in collecting the field data for this study.

Michigan, was marked and cut. Sugar maple comprised 99 per cent of the stems and the net volume. We marked this stand to successively lower residual densities of 90, 70, 50, and 30 square feet of basal area per acre in trees over 10 inches d.b.h. Each level was marked separately. Thus the uncut stand of 110 square feet of basal area per acre first was marked down to 90. Then this residual stand was marked to a level of 70 square feet. This same procedure was followed for each stocking level, a different paint color being used each time.

In selecting the trees to be cut in each stocking level, we adhered to the recommendation that Arbogast (1957) proposed for marking northern hardwoods under the selection system. The following factors were considered: risk, cull, form, species, crown position, and size. Each tree was numbered and its diameter, merchantable height, and cull class were recorded. Gross tree volume was obtained by applying the composite volume tables developed by Gevorkiantz and Olsen (1955). Net sawlog volume was determined by applying the cull system devised by Zillgitt (1946).

Logging, scaling, and grading.—After all the merchantable-sized trees had been marked and classified, the stand was cut. Each stocking level class was cut separately. Since one objective of this study was to determine the timber value in each stocking level, all trees were bucked to yield the highest grade.

Logs were scaled according to the instructions given in the National Forest Scaling Handbook (U.S. Forest Serv., 1941), using the Scribner decimal C rule. Each sawlog was graded by the system recommended by the Forest Products Laboratory (U.S. Forest Serv., 1949). From these measurements the net volume by log grade was obtained for each stocking level.

Appraising stumpage.—Stumpage rates were determined so that we could compare the differences in both cut and residual stand values which were attributable to stocking levels. Since the logs were sold on the basis of quality, a different stumpage value was computed for each log grade.

In order to develop reasonable stumpage rates we first had to investigate local lumber prices. The lumber-grade price data used in this study were based solely on sugar maple and were as follows:

Lumber Grade	*Dollars/M.B.F.*
Firsts and Seconds	205
Select	180
No. 1 Common	130
No. 2 Common	75
No. 3A Common	52
No. 3B Common	30
Timbers	52

The average lumber value for each log grade was ascertained by applying the above lumber values to the data listed in tables 12–14 of the Forest Products Laboratory Report D 1737 (U.S. Forest Serv. 1949). Thus we found that grade-1 sawlogs with an average scaling diameter of 15 inches should yield lumber worth $124 per M.B.F. Grade-2 logs with an average scaling diameter of 14 inches should yield lumber worth $90 per M.B.F. And the lumber from grade-3 logs with an average scaling diameter of 13 inches should be worth about $60 per M.B.F.

Stumpage values were determined in the following maner: The average lumber value for each log grade was increased slightly to allow for slab sales and overrun. These new values express the average selling price of the lumber on a log-scale basis. Logging and milling costs and operator's profit were then deducted from the average selling price to get the following stumpage rates:

Log Grade	*Stumpage Value*
1	$64.12 per M.B.F.
2	33.00 per M.B.F.
3	2.86 per M.B.F.

Milling.—We did not plan to make a mill study in conjunction with this investigation of how stocking levels affect timber values. The operator, however, wanted to make his own test of lumber recovery by log grades. Therefore he sawed the logs of each grade separately and had the lumber tallied by a qualified grader. Results showed that the actual volume of lumber sawed overran log scale by 2 per cent but underran expected lumber recovery by 2 per cent (Tab. I). However, the actual value of the sawed products, $2,588, was 6 per cent higher than anticipated. Part of this increase was due to the practice of sawing railroad ties from the hearts of the grade-3 logs, thereby upgrading the value.

TABLE I

COMPARISON OF EXPECTED LUMBER RECOVERY WITH ACTUAL LUMBER YIELDS

Lumber Grade	Log Grade 1		Log Grade 2		Log Grade 3		Total, All Log Grades	
	Expected[1]	Actual	Expected	Actual	Expected	Actual	Expected	Actual
FAS	1,436	1,295	648	375	44	53	2,128	1,723
Sel.	750	1,442	683	784	109	139	1,542	2,365
1 Com.	1,778	1,374	3,403	3,111	1,510	1,380	6,691	5,865
Total: 1 Com & btr.	3,964	4,111	4,734	4,270	1,663	1,572	10,361	9,953
2 Com	716	724	2,465	3,021	2,615	2,686	5,796	6,431
3A Com	262	616	949	1,919	1,390	2,857	2,601	5,392
Total: 2 & 3A Com	978	1,340	3,414	4,940	4,005	5,543	8,397	11,823
3B Com	814	—	3,195	1,908	5,175	728	9,184	2,636
Tbrs.	58	204	232	238	98	2,857	388	3,299
Total: 3B Com & Tbrs.	872	204	3,427	2,146	5,273	3,585	9,572	5,935
Totals: All lumber grades	5,814	5,655	11,575	11,356	10,941	10,700	28,330	27,711

[1] Expected yields determined from lumber-grade recovery data listed in Forest Products Laboratory Report D 1737.

RESULTS

This study showed first of all that an accurate measure of net sawlog volume can be made from tree estimates. The difference between the totals of the actual scaled volume and the estimated net volume was less than ½ of 1 per cent (Tab. II). Even within a stocking level class the differences did not exceed 5 per cent. We also learned that the cull per cent was affected by stocking level. It was reduced from 29 per cent in uncut stands to 19 per cent in the 70-square-foot level. But it remained about 19 per cent until the stand was clear cut.

The total volume and value of the timber removed naturally increased as stocking level was reduced. This increase, however, did not take place at a uniform rate between stocking levels. The rate at which volume per acre was removed accelerated up to the point

TABLE II

ESTIMATED GROSS AND NET VOLUME, ACTUAL SCALED VOLUME, AND CULL PER CENT BY STOCKING LEVELS

(In board feet per acre[1])

Stocking Level[2]	Estimated Gross Volume	Estimated Net Volume	Net Volume, Log Scale	Cull Per Cent[3]
110	15,466	10,846	10,896	29.5
90	12,420	9,438	9,348	24.7
70	9,440	7,587	7,600	19.5
50	6,340	5,319	5,124	19.2
30	3,344	2,839	2,688	19.6

[1] Scribner rule.

[2] Basal area in square feet per acre for trees over 9.5 inches d.b.h.

[3] $100 - \frac{\text{net log scale}}{\text{estimated gross volume}}$

TABLE III

VOLUME AND STUMPAGE VALUE OF TIMBER CUT BY STOCKING LEVELS

Stocking Level Class[1]		Volume per Acre[2]		Value per Acre		Value per M.B.F.	
		By stocking level class	Cumulative	By stocking level class	Cumulative	By stocking level class	Cumulative
From	To	Board feet		Dollars		Dollars	
110	90	1,548	1,548	34.13	34.13	22.05	22.05
90	70	1,748	3,296	48.55	82.68	27.78	25.09
70	50	2,476	5,772	71.75	154.43	28.98	26.76
50	30	2,436	8,208	82.54	236.97	33.88	28.88
30	0	2,688	10,896	65.35	302.32	24.31	27.75

[1] Basal area in square feet per acre.

[2] Net scale, Scribner rule.

where the stand had been cut to 50 square feet (Tab. III). Thereafter it declined when we consider that the final cut removed 30 square feet instead of 20 as in other classes. Both value per acre and value per MFB of the timber removed gradually increased until the stand was cut to 30 square feet of basal area. After that both of these values declined. Timber value reached a maximum one stocking level below

timber volume because of the high-quality trees still retained at 50 square feet.

Residual net volume was correlated with stocking level, but differences between levels were not uniform (Tab. II). Above 70 square feet the difference in volume per acre between stocking levels was about 1,650 board feet. Below 70 square feet the difference between levels was more than 2,400 board feet per acre.

The effects of stocking level on residual volume can be expressed in another manner: a ratio showing net board-foot volume per square foot of residual stocking. A series of ratios were developed for the stocking levels used in this study. They showed a curvilinear relationship in net log scale attributable to stocking level. These ratios, shown below, indicate that a stocking level of 70 square feet gave the best results because the residual stand contained 109 board feet for each square foot of basal area.

Stocking Level (Sq. ft. per acre)	*Ratio* (Bd. ft. per sq. ft.)
110	99
90	104
70	109
50	102
30	90

Now to consider the effects of stocking levels on residual stumpage values. First, we found that the proportion of the residual volume in each log grade was nearly the same for each stocking level. Proportionate net volumes in log grades 1, 2, and 3 were almost identical for stocking levels of 50, 70, and 90 (Fig. 1).

Next, we found a curvilinear relationship between stumpage value per acre and residual stocking level. As stocking levels are reduced uniformly, residual stumpage values get progressively lower (Fig. 2). The 70-square-foot level appears to be the point where further cutting reduces stumpage values rather sharply.

And finally, we found that residual stumpage values per MBF had only moderate variations due to stocking levels. As shown in the following tabulation, the highest values in both dollars per MBF and dollars per square foot occurred with a residual stocking of 70 square feet.

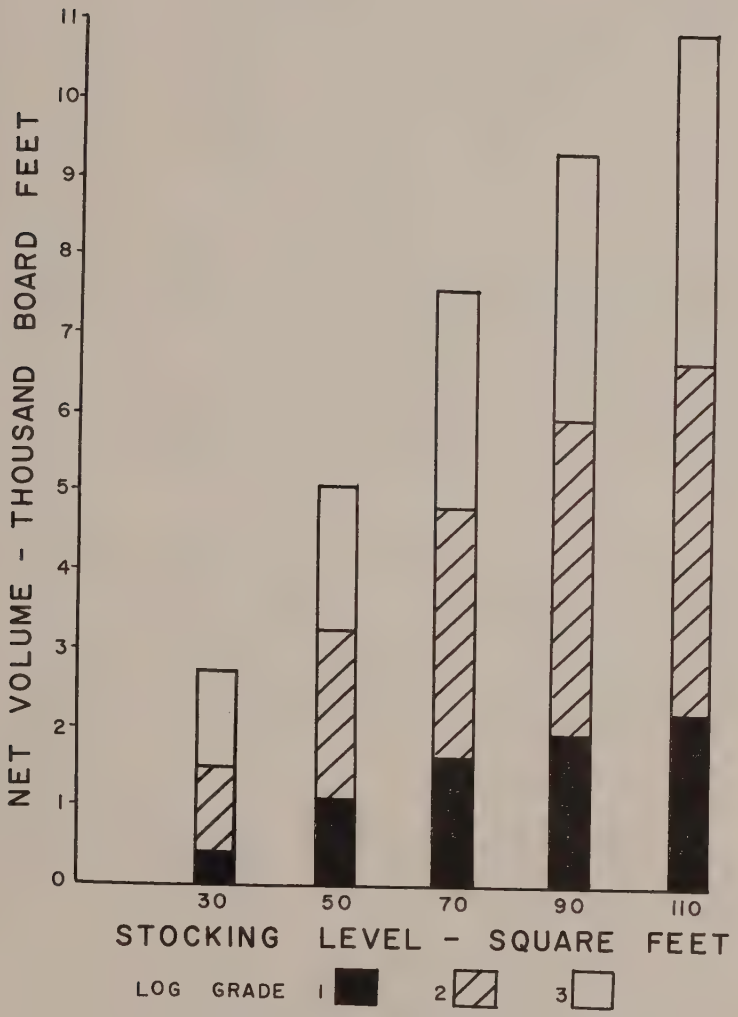

FIG. 1. Residual net volume per acre by log grade and stocking level.

Residual stocking level	*Stumpage value of residual stand*	
(Sq. ft. per acre)	(Dollars per M.B.F.)	(Dollars per sq. ft.)
110	27.75	2.75
90	28.69	2.98
70	28.90	3.14
50	28.86	2.96
30	24.31	2.18

Expressing residual stand value in terms of dollars per square foot of basal area portrays net worth by stand density. Dense stands above 70 square feet had more cull, so the value per square foot was lower. In stands with a lighter stocking the trees and logs were smaller and of lower value than those in the 70-foot level. It is evident, therefore, that the value of an old-growth northern hardwood stand can be immediately improved by applying recommended marking techniques and cutting to the recommended stocking level of 70 square feet.

Summary

1. Accurate sugar maple sawlog volumes can be obtained from tree estimates. Differences between scaled volumes and estimated volumes were less than 5 per cent.

2. Stocking level cuttings affected the amount of cull in old-growth northern hardwood stands. Cull was reduced from about 30 per cent in uncut stands to about 20 per cent in stands cut to a residual basal area of 70 square feet per acre. The cull per cent remained constant below this level.

3. The highest returns per acre were obtained when the stand was clear cut. But both the volume and value of the timber removed fluctuated with uniform changes in stocking level. There was an increase in the volume per acre removed between stocking levels until the stand had been cut to 50 square feet of basal area. When the stand was cut below 50 square feet, there was a decline in the volume removed per square foot of residual growing stock. The value per MBF cut increased until the original stand had been cut back to 30 square feet. Then it declined because of small log size.

4. Residual volume was related to stocking level but was not perfectly correlated. Volume differences between stocking levels were

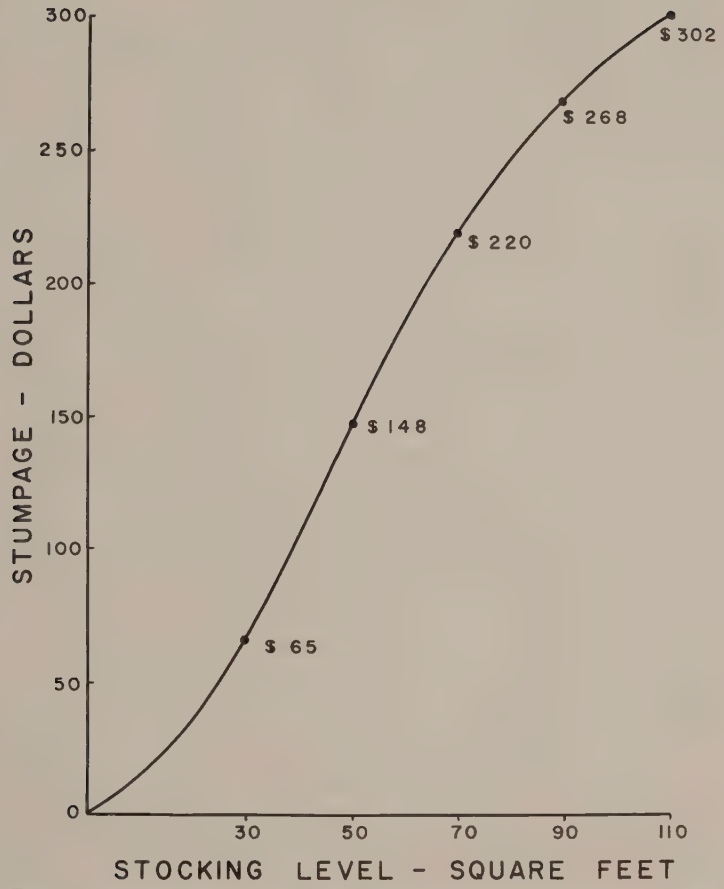

FIG. 2. Per acre stumpage value of the residual stand at various stocking levels.

smaller above 70 square feet than they were below this level. The proportion of the volume in log grades 1, 2, and 3 was almost identical for stocking levels of 50, 70, and 90 square feet.

5. The ratio of net board-foot yield per square foot of residual stocking was highest at the 70-square-foot level. At this stocking the stand yielded 109 board feet for each square foot of basal area.

6. There was a curvilinear relationship between residual stumpage value per acre and stocking level. Stands cut below 70 square feet showed a rapid decline in residual valuation.

7. Residual stumpage values in terms of dollars per MBF and dollars per square foot varied moderately but were highest for stands cut to a stocking level of 70.

LITERATURE CITED

ARBOGAST, CARL, JR. 1957. Marking Guides for Northern Hardwoods under the Selection System. Lake States Forest Expt. Sta., Sta. Paper 56, 20 pp., illus.

EYRE, F. H., AND W. M. ZILLGITT. 1953. Partial Cuttings in Northern Hardwoods of the Lake States. U.S. Dept. Agr. Tech. Bull. 1076, 124 pp., illus.

GEVORKIANTZ, S. R., AND L. P. OLSEN. 1955. Composite Volume Tables for Timber and Their Application in the Lake States. U.S. Dept. Agr. Tech. Bull. 1104, 51 pp., illus.

U.S. FOREST SERVICE. 1941. National Forest Scaling Handbook. 101 pp., illus.

——, Forest Products Laboratory. 1949. Hardwood Log Grades for Standard Lumber. Forest Prod. Lab. Rpt. D1737, 15 pp., 48 tab., illus. (Processed.)

ZILLGITT, W. M. 1946. A Quick Method of Estimating Cull in Northern Hardwood Stands. U.S. Forest Serv., Lake States Forest Expt. Sta. Tech. Note 255, 1 p. (Processed.)

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WILDLIFE

WINTER DEER MORTALITY ON TWO PRIVATE HUNTING CLUBS*

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The winter of 1958–59 was severe in the northern Lower Peninsula of Michigan. At the Houghton Lake Wildlife Experiment Station in Roscommon County, monthly temperature means remained below normal from December through March. Total snowfall was 71 inches, 20 inches over the average for that of the preceding 5 years. Snow depth reached 28 inches in February and remained nearly that great during most of March. Days with 12 inches or more of snow on the ground totaled 64, contrasting with the previous 5-year average of 12. In February and March 1959, there were 39 days with snow 20 inches or deeper. Records from other stations depict similar severity, or worse, over the entire region.

These conditions brought serious starvation to much of the state's deer herd. In order to assess the expected losses the Game Division carried out a state-wide dead deer survey in April immediately after the snow was gone. The survey was based on sampling and searching procedures developed by the division's biometricians (Ryel, 1959). The results provided good estimates of the total winter mortality of deer in both peninsulas.

During this same time an opportunity arose to apply the survey method on 2 large hunting clubs where we suspected a severe die-off. The purpose of this paper is to report on the application of the method on these township-sized areas and to present estimates of the deer mortality that occurred on them.

* A report on a joint effort of (a) the Wildlife Management Department, School of Natural Resources, University of Michigan, (b) the American Boxboard Division, Packaging Corporation of America, and (c) the Game Division, Michigan Department of Conservation. The Game Division participated through Federal Aid to Wildlife Restoration Projects W-95-R and W-96-R. Special thanks are due the Turtle Lake and Mid Forest Lodge hunting clubs for their courtesies.

The areas are 2 of the largest private hunting clubs in the state: Turtle Lake Club with about 27,000 acres (42 sq. mi.) and Mid Forest Lodge with 18,000 acres (28 sq. mi.). Both clubs during the past several years have begun managed harvesting of pulpwood under agreement with the Packaging Corporation of America. The University of Michigan's School of Natural Resources, in its deer-aspen research program, has recently initiated intensive studies on both areas to assess the effects of large-scale forest management on deer herds. The Game Division, being vitally concerned in this aspect of deer range management, is coöperating in the studies. The three agencies, having a common interest, joined forces to conduct the surveys here reported. Both of the clubs provided lodging and meals for the crews making the survey and, on the Mid Forest Lodge, a number of club members participated in the search.

Description of areas.—The Turtle Lake Club is about equally divided between the southeast corner of Montmorency County and the southwest corner of Alpena County, with a small part in the northeast corner of Oscoda County. Its history as a private hunting club goes back over 70 years to the era immediately following logging. The vegetation is largely the second-growth forest typical of the region: aspen, oak, jack pine, northern hardwoods, and swamp conifers. White-tailed deer (*Odocoileus virginianus borealis*) have been overabundant on the club for a long time. Bartlett (1950) describes the area as being the nucleus of an overpopulation of deer which has now spread across 17 counties. Starvation and deterioration of winter yards were evident as early as 1930. Preferred browse has long been exhausted on the uplands as well as in the wintering yards of the swamps. The yards afford virtually no deer food of any quality, and, in a winter of any degree of severity, starvation reaps a grim harvest.

The club has a quite limited membership, and the hunting season harvest is accordingly very light, probably not more than 2 deer per square mile. We can only guess at the total number of deer on the area. It is certainly extremely high and was possibly around 80 per square mile in the fall of 1958. This figure is in agreement with recent estimates of Westell (1960) and his co-workers.

The Mid Forest Lodge occupies most of a township in south central Roscommon County, about 60 miles southwest of the other club. Second-growth forest is the dominant cover here also with generally

the same types represented as on Turtle Lake, but with only a scattering of small, swamp yarding areas. The overpopulation of deer has developed more recently on Mid Forest, and the range has not deteriorated so badly as on the older club. The food shortage is serious nevertheless, with the telltale browse line much in evidence over most of the upland summer range.

In contrast to Turtle Lake, Mid Forest's larger membership harvests a more ample proportion of the deer herd during the hunting season. Between 500 and 600 hunters in the past 3 years have taken an average of 160 deer per year. In the past 2 years the kill has included antlerless deer, 15 per cent in 1958 and 36 per cent in 1959 (data from the club's gate tallies).

The fall population of deer on this club was probably about 65 per square mile in 1958. Westell (1958) estimated 55 per square mile in 1957, and he felt that the population was higher the following year. These figures are agreeably close to opinions of other biologists familiar with the area.

The forest management program undertaken by both clubs in the past 6 years has two objectives: deer range improvement and sustained pulpwood production. The two are compatible as long as browsing pressure does not exceed adequate regeneration of the pulp crop (Westell, 1954). On Turtle Lake the herd has remained so large that regrowth has failed, whereas on Mid Forest the tree regeneration appears to be keeping ahead of the deer, though the margin may be slight.

The survey method.—The Game Division's Houghton Lake Wildlife Experiment Station set up the survey procedure and supervised the field work. The method was essentially the same as the one used in the division's statewide survey with only slight modification in the size of the strip.

Teams of from 3 to 5 men, walking abreast, completely searched a strip 3 chains (198 feet) wide and 1½ miles long in each sampling unit (Fig. 1). The sampling units were quarter-sections, within which the survey strips followed closed, rectangular courses, along the north and south sides of the quarter-section and ⅛ mile in from the east and west sides. Each rectangular strip, referred to as a plot, covered 36 acres.

The division's biometricians determined that a statistically usable sample would require 40 randomly distributed plots on each club.

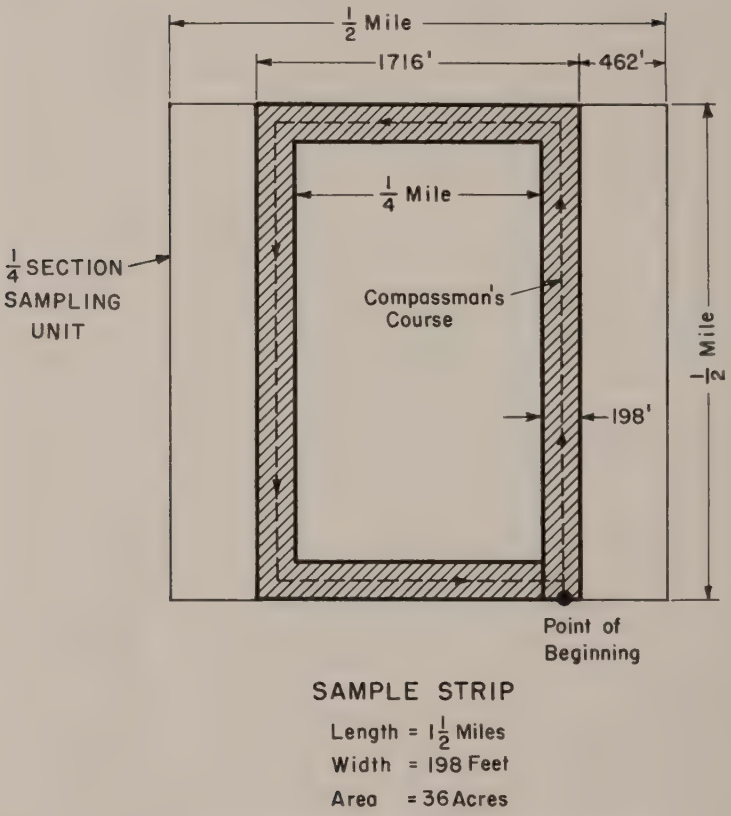

Fig. 1. The sample strip and its location in the quarter section.

Thus, on each area a complete search for dead deer would cover 1,440 acres (40 × 36 acres), or 5.2 per cent of the Turtle Lake acreage and 8 per cent of the entire Mid Forest area. The number of dead deer found on these samples, when expanded, gave estimates of the total mortality on the clubs.

To select the sample of 40 units in a completely random pattern, we numbered consecutively all quarter-sections in each area, and from a table of random numbers drew 40 numbers for each area. The

correspondingly numbered quarter-sections then became the sample units. We then plotted units on maps of the areas, and numbered each plot consecutively, 1 through 40, beginning in the northeast corner of the area. Figs. 2 and 3 show the arrangement of the sampling units on both clubs.

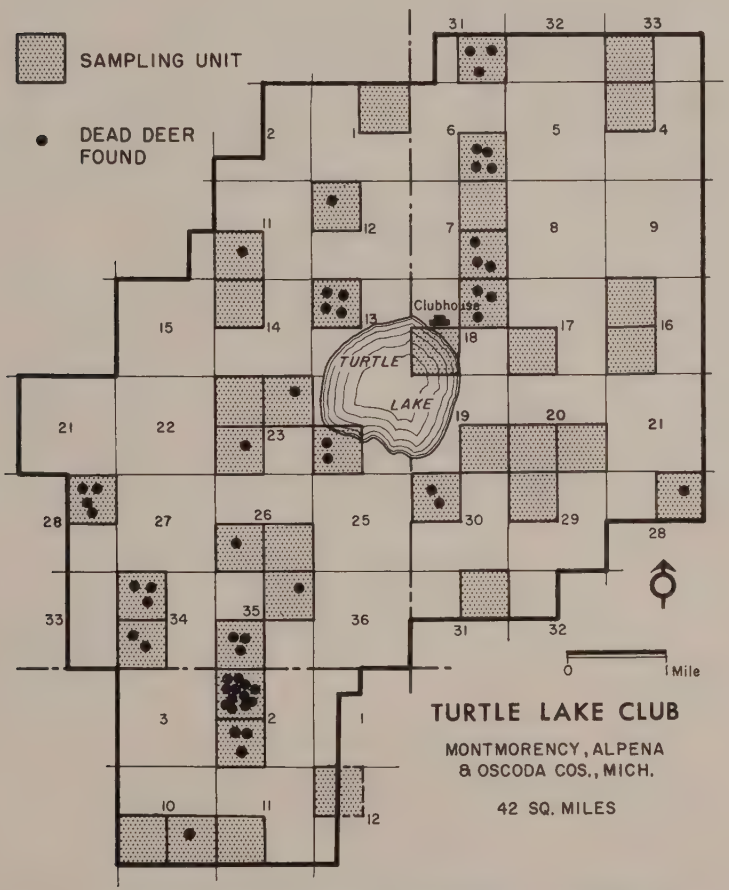

FIG. 2. The location of sampling units and the distribution of dead deer found on the Turtle Lake Club.

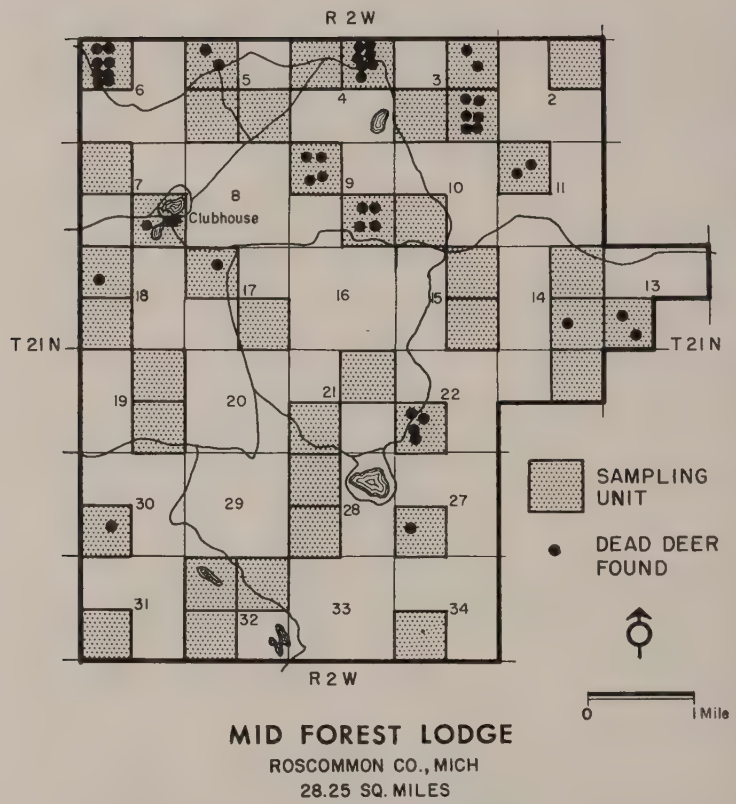

Fig. 3. The location of sampling units and the distribution of dead deer found on the Mid Forest Lodge.

On each course the assigned crew began the search at the most convenient point. The men traversed the strip, walking in line abreast, the crew leader following a compass course and pacing to measure distance. The crew tallied all dead deer found on the strip, and autopsied them to determine the cause of death. Autopsies primarily sought evidence of starvation or gunshot wounds. Whenever possible the bone marrow test (Cheatum, 1949) was the criterion of

starvation. When reasonable proof was lacking, we classified the cause of death as "undetermined." In most undetermined cases the carcasses were old and badly torn apart or eaten by scavengers. It is likely that most of them were hunting-season casualties.

On Turtle Lake we ran the survey on April 18 and 19, 1959, with 25 men in 3-man crews. We selected May 2 and 3, 1959, for the Mid Forest survey, using 33 men the first day and 38 the second, in 10 crews of 3 to 5 men each. In most cases crew leaders had previous experience in the survey method.

Findings.—We found more dead deer on Turtle Lake than on Mid Forest, 26 per square mile as compared to about 21 (Tab. I). Confidence limits were wide in both cases, about 50 per cent at the .95 probability level. The reason for this is the wide variation shown by both sets of data. On Turtle Lake where we found 56 carcasses, 20 plots had from 1 to 4 deer, 1 had 12, and 18 had none. The 47 carcasses on Mid Forest were on 16 plots, ranging from 1 to 8 per plot, and 24 plots had none. Figs. 2 and 3 show the distribution of the dead deer on both areas.

On both areas the causes of death were similar. Starvation caused 80 per cent of the mortality on Turtle Lake and 81 per cent on Mid Forest. Gun-shot deer on Turtle Lake comprised 7 per cent of the total and on Mid Forest, 6 per cent. On both areas we were unable to establish the cause of death in 13 per cent of the deer found.

TABLE I

Summary of Findings on Dead Deer Surveys, Spring 1959

	Turtle Lake Club	Mid Forest Lodge
Area of club	26,900 acres	18,080 acres
Number of sample plots	39	40
Size of sample area	1,404 acres	1,440 acres
Proportion of club sampled	.052	.080
Mean no. dead deer per plot	1.436	1.175
Standard error of mean	.354	.324
Two S.E. as proportion of mean	.493	.534
Average no. dead deer per sq. mi.	25.5	20.9
Estimated mortality on club	1,071	590
Proportion starved	.804	.808
Proportion shot	.071	.064
Proportion cause undetermined	.125	.128

Fawns made up the greatest proportion of the starvation loss on both areas: 69 per cent on Turtle Lake and 84 per cent on Mid Forest (Tab. II). The greater starvation of adults on Turtle Lake very likely signifies poorer range conditions or more severe weather, or both, on that area. Among the adults, does far outnumbered bucks. A greater loss occurred in the older does, 5 to 8 years old, than in the younger ones. However, we found no very old does (9 years old and older).

Published findings of dead-deer counts in other states show some close similarities to our data, and in one case an important difference. For the most part, workers in other states did not base their surveys on random sampling of wide areas with varied cover types, and did not attempt to assess total losses on large areas. Rather, their surveys were intensive searches of limited areas aimed at determining the relative level of mortality in winter yards. The proportion of mortality due to starvation is similar to ours in several instances. In

TABLE II

Sex and Age of Starved Deer Found on Sample Plots, Spring 1959

Age Class	Turtle Lake Club				Mid Forest Lodge			
	Male	Female	Total		Male	Female	Total	
Fawns	12	16	31*	(69%)	11	21	32	(84%)
1 year								
2 year	1	1	2		1	1	2	
3 year		1	1					
4 year	1		1			1	1	
5 year		2	2					
6 year		3	3					
7 year		4	4					
8 year		1	1			3	3	
Total Adult	2	12	14	(31%)	1	5	6	(16%)
Total Deer	14	28	45	(100%)	12	26	38	(100%)

	Sex Ratio	*Sex Ratio*
Fawns	75 male:100 female	52 male:100 female
Adult	17 male:100 female	20 male:100 female

* Includes 3 fawns of unknown sex.

Wisconsin, Swift (1946) reports that in the spring of 1941, 80 per cent of 448 dead deer had starved, in 1943 starvation accounted for 82 per cent of 1,428 deer. Also in that state, Dahlberg and Guettinger (1956) refer to a 1949 search where starvation amounted to 77 per cent, and a 1950 instance of 84 per cent. They present figures for one deer yard of 5 to 6 square miles that indicate a loss of 40 deer per square mile in a particularly severe winter. Severinghaus (1947), in relating starvation losses to winter severity, refers to a year of high mortality when searches turned up 21.8 dead deer per square mile with fawns and adults about equal, and a year of moderate loss of 12 deer per square mile, of which two-thirds were fawns.

Taylor and Hahn (1947) report high die-offs from starvation among white-tailed deer in central Texas and cite a survey of a 71,000-acre area where an estimated 30 deer per square mile starved.

The unbalanced sex ratio of fawns found in our surveys differed from findings reported by Dahlberg and Guettinger (1956) in Wisconsin. On both of our areas more female fawns starved than males—75 males:100 females on Turtle Lake and 52:100 on Mid Forest. The Wisconsin figures show an even sex ratio. In the west, Columbian black-tailed deer mortality shows an excess of males starving, 139 males:100 females (Taber and Dasmann, 1954). On the other hand Robinette et al (1957) found starved mule deer fawns in ratios similar to ours, 67–83 males:100 females. No clear explanations are at hand for any of these sex differentials in starved fawns.

The Game Division last year based its region-wide dead deer survey on stratified random sampling (Ryel, 1959). Unfortunately, we can make no valid comparisons between the more intensive search on the clubs and the relatively much lower sampling done on the regional scale. It is interesting to note, however, that the highest rate of mortality measured in the extensive survey was 25.5 dead deer per square mile, 67 per cent dead from starvation. This was in the high-population stratum of the district containing Mid Forest and part of Turtle Lake. Also, of all starved deer found, 84 per cent were fawns, and the fawn sex ratio was 54 males:100 females.

To estimate total mortality on the club lands we can legitimately expand the sample findings, keeping in mind the confidence limits indicated by the data. In so doing we arrived at an estimate of 1,071 dead deer (543–1,599) on Turtle Lake and 590 (275–905) on Mid Forest. Going back to the probable population levels stated earlier for

both areas, we may estimate that in the fall of 1958 there were about 3,300 deer on Turtle Lake and 1,800 on Mid Forest. From these figures both areas appear to have lost about a third of their deer during the winter of 1958–59.

Air search.—On the day after the survey on the Turtle Lake Club we had an opportunity to make an air search for dead deer. A Cessna 180 airplane with pilot and 2 observers flew 6 transects, at one-mile intervals, north and south across the entire club property. The altitude maintained was 500 feet, air speed, 100 m.p.h. The observers were able to scan in any one transect a strip approximately one quarter of a mile wide.

The tally on the strips was 25 dead deer. The area of the transects flown was 5,600 acres, or 8.7 square miles (20 chains wide x 35 miles long). We therefore observed dead deer at the rate of 2.9 per square mile. This is only 11.4 per cent of the estimated mortality based on the ground search and would yield a total loss on the club of 122 deer, obviously a very inadequate estimate.

Summary.

1. The winter of 1958–59 was severe in northern lower Michigan.

2. Through coöperation of several agencies in the spring of 1959, we conducted a systematic search for dead deer on 2 large private hunting clubs, both known to have very high deer populations.

3. On each club we made complete searches for dead deer on 39 or 40 random sample plots, each plot 36 acres in area. The method employed was similar to the one used on a region-wide survey.

4. The club with poorer deer range had lost 25.5 deer per square mile; the other club, 20.9.

5. Eighty per cent of the dead deer on both clubs had starved, and about 7 per cent had died of gunshot.

6. Fawns made up 69 per cent of the starved deer on the club with the heavier loss and 84 per cent on the other club.

7. Of the starved adults on both clubs, does far outnumbered bucks and a greater loss occurred in the older age classes of does.

8. The male-to-female ratio of dead fawns was 75:100 on one club and 52:100 on the other.

9. Both clubs lost a third of their fall population during the winter of 1958–59.

10. An air search on one of the clubs immediately after the

ground survey yielded a much lower and obviously inadequate estimate of mortality.

LITERATURE CITED

Bartlett, Ilo H. 1950. Michigan Deer. Mich. Dept. Cons., Game Div. 50 pp.

Cheatum, E. L. 1949. Bone Marrow as an Index of Malnutrition in Deer. N. Y. State Conservationist, 3(5): 19–22.

Dahlberg, Burton L., and Ralph C. Guettinger. 1956. The White-Tailed Deer in Wisconsin. Wisc. Cons. Dept., Tech. Wildl. Bull. 14. 282 pp.

Robinette, W. L., J. S. Gashwiler, J. B. Low, and D. A. Jones. 1957. Differential Winter Mortality by Sex and Age among Mule Deer. J. Wildl. Mgmt., 21: 1–16.

Ryel, L. A. 1959. Technical Report on the 1959 Dead Deer Searches. Mich. Dept. Cons., Game Div., Report 2242. 43 pp., mimeo.

Severinghaus, C. W. 1947. Relationship of Weather to Winter Mortality and Population Levels among Deer in the Adirondack Region of New York. Trans. N. Amer. Wildl. Conf., 12: 212–223.

Swift, Ernest. 1946. A History of Wisconsin Deer. Wisc. Cons. Dept. Publ. 323. 96 pp.

Taber, R. D., and R. F. Dasmann. 1954. A Sex Difference in Mortality in Young Columbia Black-Tailed Deer. J. Wildl. Mgmt., 18: 309–315.

Taylor, Walter P., and Henry C. Hahn. 1947. Die-offs among the White-Tailed Deer in the Edwards Plateau of Texas. J. Wildl. Mgmt. 11: 317–323.

Westell, Casey E., Jr. 1954. Available Browse Following Aspen Logging in Lower Michigan. J. Wildl. Mgmt., 18: 266–271.

——. 1958. A Forest and Wildlife Management Plan for the Mid Forest Lodge Club. Packaging Corp. of Amer., Amer. Boxboard Div. 67 pp., mimeo.

——. 1960. Personal communication.

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VALIDITY OF AGE DETERMINATION IN MICHIGAN DEER*

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Introduction

We are approaching the point in Michigan deer herd management where we need rather precise estimates of local populations, survival rates, and huntable surpluses. An important part of this knowledge comes to us through examination of the age structure of the hunting season kill. It is time we took stock to see if our current age determination technique—based on mandibular tooth replacement and wear—is providing us with valid age ratios. Our assessment will be based on two approaches: (1) Is the technique valid and precise within tolerable limits? (2) Assuming the technique is basically adequate, can we apply it properly?

Historical

The technique of aging animals by the teeth is an old one; for example, the remark, "Do not look a gift horse in the mouth" is credited to Saint Jerome of the 5th century. Certainly it has been common knowledge for generations that domestic animals could be aged by noting the development and wear of the teeth (Pope, 1934). It is not surprising, therefore, that early deer workers in this country turned to the dentition for separating age classes in the Cervids.

Cahalane (1932) classified 244 white-tailed (*Odocoileus virginianus*) deer skulls from Michigan's hunting season into 4 age classes by means of relative wear on the dentition. However, only one of his set was known-aged. McLean (1936) describes briefly the tooth replacement sequence in the genus *Odocoileus*, while Cowan (1936) presents it in some detail for black-tailed deer (*O. hemionus*). Park and Day (1942) indicate the progressive changes in the dental formula

* A contribution of Pittman-Robertson Projects W-96-R, Survey and Statistical Analysis, and W-70-R, Region I Game Management Research, and the Game Division Laboratory.

of the white-tailed deer up to 30 months of age, but they point out a study of a series of known age jaws would be the only means of extending accurate aging beyond 30 months.

It remained then for Severinghaus (1949) and his co-workers to make an actual collection of mandibles from known-aged deer and to describe normal wear patterns and criteria for white-tailed deer age classes up through 10½ years, and later (Severinghaus and Tanck, 1950) to 16½ years. One should consult these two papers for details on the technique.

Subsequent studies based on known-age specimens and or wear classes of unknown-age jaws have been made in mule deer (*Odocoileus hemionus*) by Robinette et al., (1957), elk (*Cervus canadensis*) by Murie (1951) and Quimby and Gaab (1957), and moose (*Alces alces*) in Peterson (1955).

After publication of Severinghaus' work, we initiated a program in Michigan to collect numbers of lower jaws during the 1950 hunting season. Severinghaus himself examined and aged a part of these when he visited Michigan in 1951, and Tanck, also of the New York Conservation Department, aged another group for us at the 1953 Northeast Game Conference. Using these aged mandibles as the standard, we put together reference sets on "jaw boards" containing a representative example of each year-class to use as guides for age determination. We are interested primarily, of course, in the age classes found in November during the regular gun hunting season, that is, ½, 1½, 2½, and so on, since our deer are born in late spring and early summer.

In 1951 we began experimentally to determine the age of a sample of deer killed in the hunting season by examining deer at roadside checking stations, locker plants, and special study areas, and on islands (Anon., 1952). Large scale biological data collections began in 1952 and have continued each hunting season to date. In addition, during this period we have built up a collection of 120 known-age deer jaws ranging from 5 months to 12½ years.

When he worked out his techniques for age determination Severinghaus (1949) had available specimens of known-age deer only from New York. Since then Severinghaus and Cheatum (1956) report that they have examined white-tailed deer jaws from several other states and found that wear patterns in general were similar to their collection. They conclude, however, that: "The aging criteria de-

scribed still must be subjected to critical review based on further collections of known-age specimens. Their applicability can be made more adequate and reliable by a conscientious reporting of material that agrees or disagrees wth present concepts." This paper is an attempt to do this with the material we have available on Michigan deer. We have evidence of three types on which to base our evaluation: (1) tests of aging skill from 1955 to 1959, (2) the biological data gathered since 1951, and (3) the collection of known-age mandibles.

Aging Tests

Prior to the deer season each year, we conduct a half-day refresher course in deer aging for all our collectors of biological data concerning deer shot by hunters. First Fay presents an illustrated talk on the technique. Then follows a practice period with a collection of aged and labeled jaws having several examples of each year-class. A test concludes the session.

The tests reflect our degree of success in conforming to a standard, whether or not this standard is valid. Assigning jaws to various age classes based on progressive wear must be necessarily a subjective process. Doubtless a given jaw produces a different image in the minds of different workers. In Michigan we must use many different individuals to man our checking stations. We need to know something of the variability we can expect between agers in order to interpret properly the data derived from examination of the kill. The alternative is a system of jaw collection to permit one or a few men to do all of the aging, but this would not be practical for us. Flyger (1958) has proposed a system of making impressions of the teeth with modeling clay and later positive casts from these molds so that a few men can thus do all of the aging.

Basically our test is made up of 50 jaws selected from each age class based on an annual survival of about 50 per cent (Tab. I). These proportions are a compromise between those normally observed in the Upper Peninsula and northern Lower Peninsula. We assumed that the occurrence of each age class in the population determined its relative importance, and skill in aging should likewise follow the same pattern. In addition to the 50-jaw test, we initiated a 30-jaw test in 1957, more appropriate for our antlerless deer, composed of one-third fawns, and with more practice on "middle-aged"

TABLE I

SUMMARY OF 50 JAW AGING TESTS

Year	Individuals Tested	Age Class	Number of Jaws	Frequency		Errors Made
				Observed	Expected	
1955	53	1½	22	1,109	1,166	73
		2½	11	506	583	173
		3½	6	434	318	94
		4½	5	274	265	86
		5½ & older	6	327	318	162
Total			50	2,650	2,650	588
1956	51	1½	22	1,130	1,122	50
		2½	11	512	561	158
		3½	6	408	357	88
		4½	5	226	204	105
		5½ & older	6	274	306	156
Total			50	2,550	2,550	557
1957	63	1½	21	1,289	1,323	73
		2½	12	610	756	283
		3½	7	599	441	110
		4½	4	311	252	131
		5½ & older	6	341	378	211
Total			50	3,150	3,150	808
1958	62	1½	21	1,273	1,301	51
		2½	12	672	743	174
		3½	7	519	434	102
		4½	4	314	247	121
		5½ & older	6	319	372	218
Total			50	3,097	3,097	666
1959	70	1½	21	1,437	1,470	54
		2½	12	727	840	203
		3½	6	613	420	102
		4½	5	352	350	158
		5½ & older	6	371	420	261
Total			50	3,500	3,500	778

deer. This has consisted of seven 5-months-old fawns, three 6-months-old fawns, eleven or twelve 2½-year-olds, six or seven 3½-year-olds, and two 4½-year-olds. None of the jaws used on these tests is of known age. They are merely from deer killed in the fall, carefully assigned to age classes based on Severinghaus' criteria. Some of these Severinghaus or Tanck actually aged. We have tried to use only jaws that were "typical" and exhibited "normal" wear.

Both tests have been of the "open book" type. We have encouraged reference to the labeled, aged jaws present. Compared to working at checking stations on hunter-killed deer, these tests are conducted under ideal conditions. The jaws are clean, and one can pick them up and hold them in any position. All teeth are equally visible, lighting is good, hands are warm, and time is not a factor. It is difficult to believe a person can age deer more accurately in the field than he does on these tests. Consequently, we have used the results of the tests as a guide in selecting the most adept agers for each checking station unit.

From 1955 to 1959, we have 299 scores on the 50-jaw test (89 different individuals), and from 1957 to 1959, 180 scores on the 30-jaw test (85 different people).

Some of the individual jaws appeared in the tests every year, but we did make substitutions because of breakage or discovery of more representative examples. There is a slight possibility that some people could have remembered certain jaws from one year to the next, or at any rate remembered that there were only three 5½-year-olds, two 6½-year-olds, or one 7½-year-old. At some of the testing sessions the group knew that no jaws were older than 7½ years. These three age classes and older deer do not comprise a very large part of a herd where deer experience a high annual mortality, as in Michigan. Furthermore, tooth wear patterns become increasingly variable with increasing age. Fortunately, we can determine survival rates quite well, using only the proportion of deer found in each age class up through 4½ years.

We had hoped that it would be possible to age deer consistently up through 4½ years old. The agers, however, tended to under-age 4½-year-olds (and older deer) and to over-age 5-month fawns and 1½ and 2½-year-old deer. Six-month fawns and 3½-year-old deer exhibited a fairly symmetrical distribution. Moreover there was a disturbing lack of consistency in assigning ages, particularly in the four older age classes. In Table II the figures in each row show the dis-

tribution of ages recorded on the tests for jaws which we believe actually belong to the age classes listed at the left. For example, 93 per cent of the 5-month-old jaws were correctly aged, 6 per cent were called 6-month-olds, and 1 per cent were classed as 1½-year-olds.

Another way to view the results is to note the relative accuracy with which each age is determined. That is, when agers classed a jaw in a given age class, how often were they right? The answer will vary somewhat, depending on the distribution of jaws in a given sample. Table III shows the averages for our tests. For instance, of

TABLE II

Distribution of Reported Ages by Age Class on Aging Tests

"Actual" Age	5 mo.	6 mo.	1½	2½	3½	4½	5½	6½	7½	8½	9½	10½
5 months	93%	6%	1%									
6 months	2%	94%	4%									
1½ years			95%	4%	1%							
2½ years			5%	73%	20%	2%						
3½ years			1%	18%	69%	12%						
4½ years				2%	27%	58%	11%	2%				
5½ years					3%	27%	48%	18%	3%	1%		
6½ years					1%	8%	40%	39%	10%	2%		
7½ years						1%	14%	31%	40%	11%	1%	2%

TABLE III

Average Accuracy by Age Class

Age Class	Aging Test	
	50-Jaw	30-Jaw
5 months		99.2%
6 months		86.4%
1½ years	97.6%	
2½ years	82.2%	84.3%
3½ years	50.6%	62.3%
4½ years	60.5%	53.2%
5½ years	50.5%	
6½ years	46.5%	
7½ years	59.0%	

all the jaws called 1½-years-old, about 98 per cent were actually that age.

Some misaging is normal, but what is important to us is how this affects the age ratios derived from a large number of observations. Table I implies that the mistakes made are not entirely compensating and very likely the ratios will not be very precise. Because we set up the 50-jaw tests so that the number of jaws in each age class would approximate a survival rate of about 50 per cent, differences between reported and known distributions here provide us with some notion of the errors likely in examining a sample of the kill. In every year there is a conspicuous shortage of 2½-year-old deer and a surplus of 3½- and 4½-year-old deer. Reported 1½-year-old deer and 5½-year-old and older deer, however, are near to the known distribution each year. Table I shows the number of times each age was recorded on the tests (Observed), and the number of times it should have been recorded had there been no errors in aging (Expected). There are some compensating errors here as indicated in Table II.

Have we become more proficient at aging over the years? We would like to answer "Yes" to this question, but our data does not support this conclusion. The number of errors per ager on the 50-jaw tests averaged 11, 11, 13, 11, and 11 for 1955 to 1959, respectively. Since there has been some turnover in personnel during these years, we have also compared the errors made by 22 individuals who took the 50-jaw test each of these 5 years. They averaged 10, 11, 11, 9, and 10 errors.

We have assumed that some people are innately better than others in application of this subjective technique, and we have appointed agers on the basis of test results. Using the records of the above-mentioned 22 agers, analysis of variance of test scores indicated highly significant differences between individuals ($F = 6.44^{**}$ for 21 and 88 d.f.). A multiple range test applied to the data shows several apparent levels of proficiency. These tests confirm the need for carefully selecting a few people to do the bulk of the aging where possible.

Biological Data

When discussing the biological data, it is convenient to divide the state into administrative regions and districts used by the Conservation Department (Fig. 1) with one exception. We do not sub-

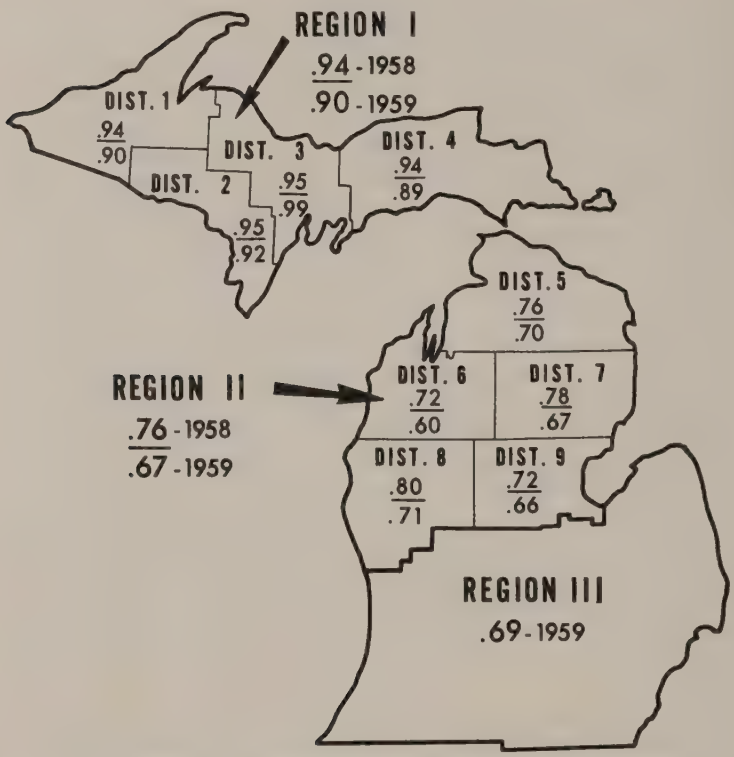


Fig. 1. Proportion of yearling bucks with milk premolars, Nov. 15–30.

divide the south half of the Lower Peninsula, Region III, because of the small number of deer examined from this area.

Our situation in Michigan is unique in that 65 per cent of the deer hunters live in the southern Lower Peninsula, while fewer than 1 per cent of the deer do. Thus, we can examine a sample of the Upper Peninsula kill at the Straits of Mackinac, and a sample of northern Lower Peninsula deer at about five checking stations on major north-south highways near the south edge of the region. Virtually all of the Game Division takes part in this venture each fall. From 1951 to 1959, we examined 80,000 deer, or nearly 10 per cent of the deer

killed by hunters in these years (Eberhardt and Fay, 1957, 1958, and 1959).

Our purpose here is a critical examination of a technique. Consequently we present only such biological data gained from its use as will give evidence of its validity. In this connection we discuss briefly the rate of tooth replacement in yearlings and apparent survival rates derived from age records of adult bucks.

Dental terminology used here follows Riney (1951). This departs from Severinghaus (1949) in that Riney considers the first premolar to be vestigial and seldom found in deer. Thus the 3 premolars present are actually P2, P3, and P4. Furthermore the "corner incisors" are really incisorform canines. During its lifetime a deer has two complete sets of incisors, canines, and premolars, a set of permanent teeth replacing the original temporary, milk, deciduous, or baby teeth. There is only the one permanent set of molars. Molars and premolars collectively compose the "cheek" teeth. Fig. 2 illustrates the location and appearance of tooth types and topography.

Yearling Tooth Replacement

In 1958 and 1959 we carried out a simple experiment to see if the tooth replacement rate differed in various parts of the state. This consisted of classifying all 1½-year-old deer examined into two groups, those with milk premolars remaining in either part of the lower jaw (1½−), and those without milk premolars (1½+).

There was a very distinct difference between the Upper and Lower peninsulas (Fig. 1). Table IV presents the numbers of deer involved

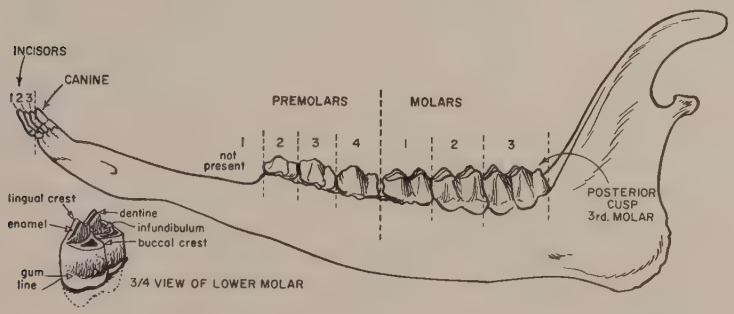


Fig. 2. White-tailed deer mandible showing terminology of dentition.

TABLE IV

PROPORTION OF YEARLING DEER HAVING MILK PREMOLARS

Area	1958				1959			
	Males		Females		Males		Females	
	Total deer	Prop. with milk pre-molars	Total deer	Prop. with milk pre-molars	Total deer	Prop. with milk pre-molars	Total deer	Prop. with milk pre-molars
District 1	252	.937	19	.895	81	.901	23	.957
2	189	.947	15	1.000	71	.916	15	.867
3	389	.946	57	.860	119	.991	37	.919
4	537	.935	18	1.000	220	.891	34	.882
Region I	1,367	.940	109	.908	491	.902	109	.908
District 5	688	.759	79	.709	262	.695	59	.576
6	438	.724	55	.745	233	.597	58	.707
7	1,253	.778	154	.734	646	.667	168	.631
8	351	.798	182	.797	319	.712	52	.654
9	401	.723	23	.870	388	.665	65	.646
Region II	3,131	.761	493	.761	1,848	.669	402	.639
Region III					346	.694		

in the various samples. We used Chi-square tests of independence of these data to test the hypotheses that two given samples are randomly drawn from a common binomial population. Chi-square values are expressed as probability for a chance deviation as great or greater than the one computed. Those with probability between .05 and .01 will be considered "significant," while a probability less than .01 will be "highly significant."

Chi-square tests comparing various samples regarding the relative frequencies of 1½− and 1½+ indicate the following:

1. No significant differences in either year for males between districts in Region I ($.80 < P < .90$).

2. A significant difference between Region II districts for males in 1958 ($.01 < P < .025$) but not in 1959 ($.05 < P < .10$).

3. Highly significant differences between years in both Regions I and II for males ($.001 < P < .005$ for Region I, $P < .0005$ for Region II).

4. Highly significant differences between Regions I and II males both years ($P < .0005$ both years).

5. No significant difference between Regions II and III males in 1959 ($.40 < P < .50$). Data insufficient for Region III in 1958.

6. No significant differences between males and females in either Regions I or II in either year ($.60 < P < .70$ for Region I, 1958; $.95 < P < .975$ for Region II, 1958; $.80 < P < .90$ for Region I, 1959; $.70 < P < .80$ for Region II, 1959).

We are not sure what is responsible for the marked difference between the Upper and Lower peninsulas. We do not have any evidence that fawns are born later in the Upper Peninsula. We do have some indication from feeding studies that poor nutrition delays tooth replacement, a phenomenon noted by other workers (Hamerstrom and Camburn, 1950; Severinghaus and Cheatum, 1956; and Robinette et al., 1957). However, if this was a factor here, then the poor food areas of the Lower Peninsula should be different from better food areas, and they are not. A third possibility is that the deer are inherently different in their rate of tooth replacement. This is certainly possible, since the Upper and Lower Peninsula deer have been separated for several thousand years (Hibbard, 1951).

Differences between years within both Regions I and II could well be the result of differences in sampling. The extreme cold weather during the 1959 hunting season froze many deer carcasses so solidly that we were unable to open the jaws to determine age. We have no explanation, however, for differences found between districts in the 1958 data for Region II.

Survival Rates

Hayne and Eberhardt (1952) offer a graphical way of estimating survival rates from age distributions in deer based on Ricker's (1948) work on the dynamics of fish populations. You simply plot the logarithms of the frequencies by age class and draw a line through the points. This "kill curve" will be a straight line, barring chance sampling deviations, if there is equal recruitment into the herd each year and uniform survival each year. The slope of the line is equal to the logarithm of the rate of survival. The survival rate can be determined mathematically or with less precision visually.

Few wild deer populations can satisfy these conditions entirely be-

cause hunting pressure, fawn production, fawn survival, and vulnerability may vary from one year to the next. Still, unless there are extreme fluctuations, this method should provide approximate measures of survival. We will discuss only survival rates for adult bucks since we do not have equivalent data for antlerless deer.

One source of error has been reduced vulnerability of 1½-year-old bucks. In some cases this produces a curve with an ascending left limb but with fairly uniform survival from the 2½-year-old class on. This was true of Adirondack deer in New York (Hayne and Eberhardt, 1952) and is also evident in deer from parts of Michigan, especially Region I (Eberhardt, 1958). The cause for this seems simply that many yearling deer fail to grow conspicuous antlers due to malnutrition, and hunters do not readily recognize them as legal game. After severe winters in areas with poor browse supplies, many bucks do not even develop antlers three inches above the skull, the minimum legal size under Michigan regular hunting season regulations, and actually are not legal game.

A disturbing characteristic of kill curves from all areas of the state in most years is an apparent lack of deer in the 2½-year-old class and a surplus in the 3½-year-olds. Eberhardt first noticed this in the areas where it is most pronounced, Districts 6 and 8 on the west side of Region II, and Region III. This lack of 2½-year-olds, however, does not seem to be real since no shortage occurs in the next age class in the following year.

Several hypotheses could account for this phenomenon—abnormal tooth replacement, abnormal tooth wear, differential vulnerability, or mistakes in aging. Because these three areas seemed to be different, we compared data from them with the rest of Region II.

The tooth replacement rate does not appear to be different. We find no significant differences in the pooled ratios of 1½− and 1½+ deer from Districts 6 and 8 compared to the remainder of Region II in either 1958 or 1959 (Chi-square probability between .70 and .80 for 1958 and 1959). Furthermore, as mentioned above, we find no significant differences in ratios between Region II and Region III in 1959.

If tooth wear were responsible, we would have to assume that once a deer has all of his adult teeth, tooth wear in these three areas was more rapid. We have no data to confirm or deny this, but we would

expect the reverse to be true since food conditions in these areas average better than in the remainder of the state.

We also have no reason to believe that the vulnerability of 2½-year-olds is different in different parts of the state. Malnutrition does retard antler development, but this occurs primarily in 1½-year-old bucks. Reduced vulnerability of the 1½-year-old deer would tend to inflate 2½-year and older age classes, however, not reduce them.

The differences found are probably not due to differences among agers. Age ratios for Districts 6 and 8 from deer examined at three checking stations in the east half of the state apparently did not differ from those obtained at two others in the west half of the state (Chi-square $.40 < P < .50$ for District 6 in 1958; $.05 < P < .10$ for District 8 in 1958; $.30 < P < .40$ for District 6 in 1959; $.10 < P < .20$ for District 8 in 1959).

There remains then the possibility that over-all mistakes in aging are responsible. To test this, we plotted the kill curve for a theoretical population having a uniform annual survival rate of 20 per cent and a uniform recruitment each year—the "expected" curve in Fig. 3. On the same graph we also plotted data for the same population but assigned deer to age classes based on the distributions in Table II. This curve exhibited an apparent shortage of 2½-year-olds and a surplus of 3½ and older deer, very similar to the lines of Districts 6 and 8 and Region III ("aging error" curve in Fig. 3). Actually in this example it happens that 2½-year-olds are close to the correct proportion while the 3½-year and 4½-year age classes are inflated. This, however, varies depending on the survival rate. Furthermore, under field conditions the difficulty of seeing the critical posterior teeth would cause more 2½-year-olds to be classed as 3½-year-olds.

We still have not accounted for the fact that kill curves from other areas are generally straighter at least from the 2½-year age class. The one difference between the two sets of areas that we can demonstrate involves winter food supplies and improved condition of deer. Yearling males from Districts 6 and 8 and Region III average larger antler beam diameters, more antler points, and greater body weight than those from other areas of the state (Eberhardt and Fay, 1959).

We can get a typical curve by assuming that only 80 per cent of the yearlings in our hypothetical population are vulnerable because

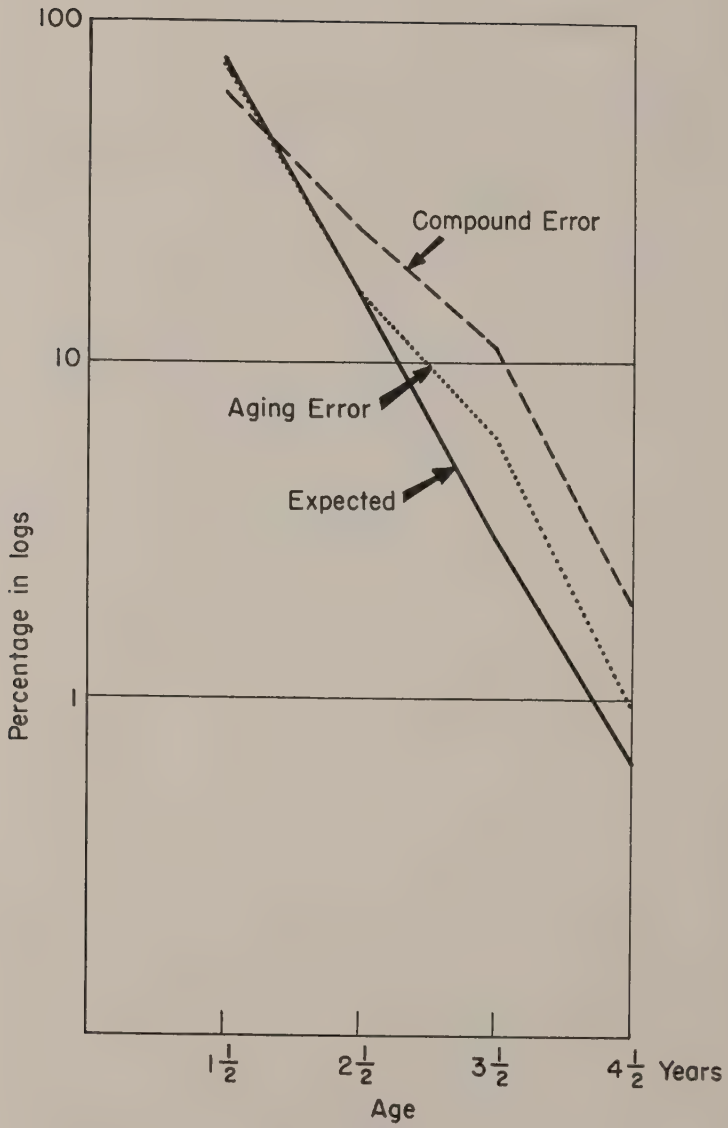


FIG. 3. Some hypothetical kill curves.

of small antlers ("compound error" curve in Fig. 3). Again we assigned deer to age classes based on distributions given in Table II. Note how much higher the apparent survival rate determined from this curve is than the actual 20 per cent.

Based on this evidence we must conclude at the present time that the survival rates we have observed in the kill are probably subject to some question simply on the basis of individual aging errors, and one must be careful in applying them too literally.

Known-Age Deer

Materials.—Perhaps the most valuable source of information for evaluation of our current deer aging is our collection of jaws from deer of known age. Since 1950 we have obtained some 120 such mandibles. These are from three sources: (1) fawns trapped, tagged, and released when newborn or 6–10 months of age, largely from 1940 to 1953, and later recovered; (2) deer from deer management studies in a 647-acre enclosure consisting of natural year-around deer range; and (3) penned deer from controlled nutrition studies. The age of the deer is a matter of record, and we carefully label each known-age jaw with an age determined from trapping and autopsy records.

With two exceptions, all deer were originally trapped by the staff of the Cusino Wildlife Experiment Station in either T46N R17W, Alger County, or T46N R16W, Schoolcraft County, in Upper Peninsula. These are a deer, aged 12½ years, tagged as a fawn in 1941 in Crawford County of the northern Lower Peninsula, and a fawn reared in captivity.

In our analysis of aging characters based on these jaws, we have eliminated all penned deer through 3½ years old. We have included five older specimens, since the available samples of these ages was necessarily small. Although there seems to be no consistent differences in tooth development or wear between penned deer and wild deer, individual animals sometimes develop abnormal wear from chewing wire fencing, sand, or small stones. Others may have been fed artificial diets such as pelleted food or corn for varying lengths of time, rather than natural browse. We have also noted that deer fed low quality diets in our nutrition studies tend to have retarded tooth development.

We have also eliminated from consideration a few malformed jaws and a number of jaws between 2½ and 5½ years more than one month older or younger than the half year. For instance, of the deer

between 3 and 4 years old, we included only those aged 3 years 5 to 7 months. Commencing with the 6-year-olds, however, we used all available known-aged jaws so that three of eight such jaws fell outside the above limits.

We are left then with 89 jaws: 42 from wild deer tagged and later recovered; 42 from deer confined for all or part of their lives in the large enclosure; and five deer in the 4½–6½ year classes confined all their adult lives in study pens and fed natural browse diets supplemented periodically by concentrated foods. Four of the last group were wild-born fawns trapped in winter, and one was born and reared in captivity.

In our evaluation we examined all material in each age class and noted those characteristics that appeared to be constant and uniform. We have also prepared a numerical summary of eruption and wear of the mandibular cheek teeth by means of tooth measurements (Table V) patterned after a similar table by Severinghaus (1949) to enable a comparison between his New York specimens and ours. His procedure was as follows:

> These measurements were from the highest point on the lingual crests of each tooth to the lowest point of heavy pigmentation along the gum line. On the premolars one measurement on each tooth was taken. On the first and second molars each lingual crest was measured (two on right and two on left jaw bones) and the average recorded. On the third molar each of the anterior lingual crests was measured and averaged. Because the posterior cusp of the third molar did not show growth and wear consistent with the other crests of this tooth, it was recorded separately.

We discuss here replacement and wear patterns of the several tooth types as revealed by our known-age collection, together with comparisons with New York deer. Our data in general substantiates the usefulness of the dentition to determine deer age. However, it suggests that there are geographical differences in both replacement rate and wear.

Incisors and canines.—Severinghaus describes the early development of dentition in white-tailed deer in some detail. At birth all incisors and canines are present. These milk teeth are present until the age of 5 or 6 months, when permanent teeth replace the central pair of incisors (I1). In New York by the sixth month, generally, this central pair are fully erupted (Fig. 4). In our sample of twelve 6-month-old jaws, however, eight retained all temporary incisors, while

TABLE V

AVERAGE HEIGHT OF LINGUAL CRESTS ABOVE GUM LINE

Age	No. of Jaws	Milk Premolars			Adult Premolars			Molars			
		2	3	4	2	3	4	1	2	3	4*
5–6 mo.	12	4.0 (3–5)†	3.9 (3–5)	5.7 (5–7)				9.0 (8–10)			
7 mo.	1	3.5 (3–4)	3.5 (3–4)	5.0				9.0	1.0		
8 mo.	1	4.0	4.0	5.0				9.0 (8–10)			
8½ mo.	1	4.0	4.0	5.0				8.0	7.5 (7–8)		
9 mo.	2	4.0	4.7 (4–5)	6.0				8.7 (8–9)	5.0 (4–7)		
10 mo.	3	3.5 (3–4)	3.8 (3–5)	5.0 (4–6)				9.0 (8–10)	5.7 (3–7)		
1 year, 6–7 mo.	16	3.5 (2–5)	3.4 (2–5)	4.6 (3–7)				8.7 (7–11)	11.2 (9–13)	7.5 (4–11)	.2 (0–2)
2 yrs., 6–7 mo.	20				4.8 (4–6)	6.4 (5–8)	7.9 (6–9)	8.2 (6–11)	10.0 (8–11)	10.0 (8–12)	4.5 (3–7)
3 yrs., 6–7 mo.	14				5.2 (4–6)	6.2 (5–8)	7.8 (5–10)	7.6 (5–9)	9.7 (8–11)	10.2 (8–12)	5.8 (4–8)
4 yrs., 6–7 mo.	4(1)‡				5.5 (5–6)	6.1 (5–7)	7.4 (6–9)	7.4 (6–9)	9.2 (8–10)	10.0 (8–11)	5.2 (4–6)
5 yrs., 4–8 mo.	5(2)				4.7 (3–6)	5.6 (4–7)	7.4 (6–9)	7.5 (6–10)	9.2 (7–11)	9.8 (8–12)	6.1 (5–8)
6 to 6½ years	3(2)				4.8 (4–6)	5.0 (4–6)	6.8 (5–8)	6.3 (5–7)	8.7 (7–10)	8.5 (8–9)	5.8 (5–7)
7 yrs., 9 mo.	1				4.5 (4–5)	4.0	5.5 (5–6)	5.0	7.0	8.0	7.0
8½ yrs.	1				5.5 (5–6)	4.5 (4–5)	5.0	5.0	8.0	9.0	7.0
9½ yrs.	1				5.0	5.0	6.0	6.0	8.0	Broken	Broken
11 yrs., 10 mo. to 12½ yrs.	2				5.0	4.5 (4–5)	5.0 (4–6)	4.2 (4–5)	6.0 (5–7)	8.0 (7–9)	6.0 (5–7)

* 3rd cusp, 3rd molar.
† Range.
‡ Penned deer included.

three had replaced the central pair with permanent teeth, and one had lost the temporary teeth but had not grown new ones. Three fawns 7 to 8 months old all had permanent first incisors.

It is pertinent here to mention the pattern of incisor replacement in the fall population that we find in our checking station records. In the Upper Peninsula the peak of fawning is between May 31 and June 10 (Haugen and Davenport, 1950) and available data suggests it is similar to Region II. For several years we have tallied fawns as

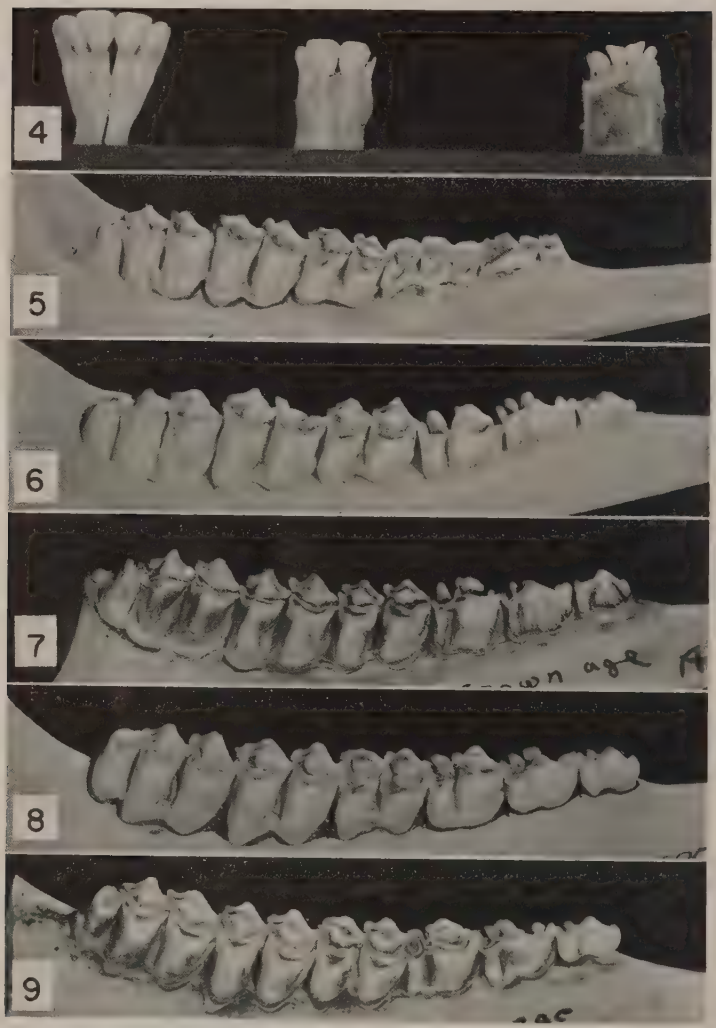


FIG. 4. Incisors and canines, from left: all permanent, 1½-year old; I 1 permanent, 8 months old; all temporary, 6 months old.

FIGS. 5–9. Known age mandibles 1½, 1½, 2½, 3½ and 4½ years old.

TABLE VI
APPARENT FAWN AGE
1959 Special Deer Seasons

Apparent Age	Region I		Region II	
	Males	Females	Males	Females
5 months	188	152	254	186
6 months	457	404	310	217
Total	645	556	564	403

"5 months" or "6 months," depending on whether the central incisors had been lost, but 1959 was the first year where the distribution of fawns in both peninsulas was adequate, due to the extent of special antlerless seasons (Tab. VI). We found that 28 per cent of Upper Peninsula fawns and 46 per cent of northern Lower Peninsula deer had lost one or both central incisors. These differences between regions are highly significant, Chi-square probability less than .0001. No difference was noted between the sexes within each region. This again points to the possibility that fawns are born earlier in Region II, but we have no evidence of this. Since there appears to be a difference in the timing of first incisor replacement between our Upper Peninsula fawns and those in New York, a similar difference could be present between Regions I and II.

According to Severinghaus, deer have a complete set of permanent incisors (and canines) by the 10th or 11th month. In our collection we have three jaws between 12 and 14 months, all of which had permanent incisors and canines.

Premolars.—In Michigan all milk premolars are erupted fully long before a fawn reaches his first hunting season. In New York, a full set of temporary premolar dentition is typical before the third month. Normally, by November, 5–6 months of age, the third and fourth temporary premolars show moderate wear. The deer retain these teeth until about 1½ years old when permanent teeth gradually replace them. In New York, deer shed these teeth around the 18th month. In our sample all 14 known-age 1½-year-old deer collected during the November 15–30 hunting season retained temporary premolars. One animal taken the last of December retained a full

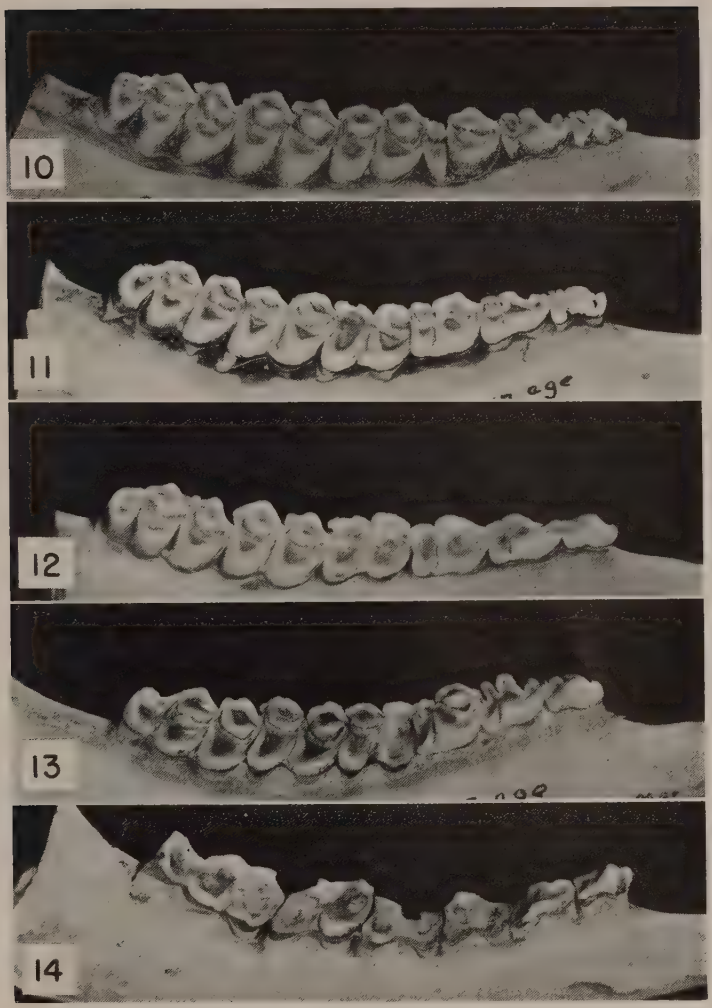
set of temporary teeth, and a second taken in mid-December retained temporaries on one side and had lost them on the other, but new teeth had not erupted. A 20-month-old animal taken February 29 had completely replaced the premolars, but these showed only a little discoloration, suggesting that they were of recent origin. We have already noted in the section on yearling tooth replacement that less than 10 per cent of the Upper Peninsula yearlings examined at checking stations had shed their milk premolars, while in the Lower Peninsula this has averaged 24 and 33 per cent for two seasons.

Premolar replacement offers the best single criterion for determining age of 1½-year-old deer. The temporary fourth premolar is 3-parted or lobed in contrast with its successor, a much larger 2-lobed tooth (Figs. 5 and 6). The temporary premolars at age 1½ normally exhibit extreme wear, especially P4. If premolar replacement has taken place, the new teeth may or may not have fully erupted. If erupted, there is little or no visible wear, and generally they show less stain than the molar teeth. By 2½ years there is normally slight to moderate wear on P3 and P4; however, wear on both is variable. In over half the specimens examined there was no dentine visible on the anterior surface of P3.

The wear by 3½ years is extremely variable and in some instances P3 and P4 may be nearly flat, while other specimens show extremely little wear. A small to moderate dentine line on the anterior surface of P3 is the only constant premolar characteristic of this age group.

Beyond 3½ years, no constant wear pattern is discernible. The second premolar usually is not worn as much as P3 and P4. Even in the older age classes, wear on this tooth is not great (Tab. V). Generally, by age 6½, most of the lingual crests of P4 are worn away, but in old age this tooth and the first molar exhibit extreme variations in wear.

Molars.—Molar development in deer provides additional criteria for determining ages of fawns and yearlings. In 12 deer 6 months old the first molar had fully erupted but M2 had not appeared. Two penned 6½-month-old deer both had second molars partially developed, but in our specimens from wild deer one 7-month fawn had M2 cusps barely visible, and in one 8-month fawn they had not yet appeared. In six 8½ to 10-month-old wild fawns this tooth was in various degrees of partial eruption. Severinghaus (1949) reported the first molar erupts at about three months and is fully erupted at about



Figs. 10–13. Known-age mandibles 5½, 7¾, 8½ and 12½ years old.
Fig. 14. Teeth from "old" deer of unknown age.

one year, while the second molar appears from 7 to 9 months and is fully erupted between 13 to 17 months.

By the time a deer reaches age 1½, all three molars have appeared, but M3 has not fully erupted, and the posterior cusp normally is not yet through the gum. In deer 2½ years old M3 has developed fully although the posterior cusp may appear to continue growing higher in older animals as the jaw completes its elongation. The condition of the posterior cusp is a prime characteristic for separating yearlings from 2½-year-old deer, although it is very difficult to see in the field without cutting the cheek to expose the teeth.

The wear of molar teeth offers the best criteria for age determination above 1½ years. At age 2½ very little wear has taken place on any of the molar teeth. All lingual crests are normally sharp, although degree of sharpness of the crests of the first molar varies widely. The most uniform molar criterion of the 2½-year-old class is the very limited amount of wear on M3. The lingual crests of this tooth are extremely sharp, and only a slight dentine line shows on their surfaces. The posterior cusp of M3 generally has very little wear, if any.

The most characteristic molar wear in the 3½-year class is on the posterior cusp of M3. Usually it appears either flattened, hollowed out, or both. Lingual crests of the first molar normally are blunt; those of the remaining molars remain sharp.

In 4½ years and older deer molar wear continues, but individual variation makes it difficult to describe typical wear patterns. Usually, by 6½ years, M1 is becoming flat and the tooth may be so worn that the infundibulum (central cavity between the lingual and buccal parts of each tooth) is missing or becomes a crescent-shaped line. On both cusps of M1 the infundibulum is missing in the known-age 6½-year specimens. Lingual crests of M2 and M3 remain, although somewhat flattened on all known-age specimens through 12½ years. Both the known-age 12 and 12½-year specimens have retained the infundibulum on M2 and M3. Loss of this character and complete flattening of the molars would indicate a deer of extreme age, probably 15 years or older.

Our known-age material differs considerably from that described for New York deer in regard to molar wear. Agreement is good in the 2½ and 3½-year age groups but falls off rapidly as the age increases. Lingual crests of the first molar, while blunt, are not worn away and the infundibulum on M1 is not missing in the 4½–5½-year class. Ac-

cording to Severinghaus (1949) the primary criteria in his 5½-6½-year class are the condition of the first and second molars. No lingual crests remain on these teeth. We have eight known-age jaws between 6 and 12½ years of age and only two, a 6½ and a 7¾-year-old, have lost the lingual crests of M2.

The criteria set up for the 7½-year class in New York readily fits our known-age 12½-year Michigan specimen. Furthermore our 12-year-old jaw still possessed lingual crests on M2 and M3, as well as well-defined infundibula. This particular specimen could easily fit the description for Severinghaus' 5½-year class. Pictures and descriptions in his paper of 8½-year and older animals certainly would be well over 12½ years of age in Michigan. Michigan deer with tooth wear similar to the 16-year specimen described by Severinghaus and Tanck (1950) could easily be 20 to 22 years old.

Comparison of lingual crest height above gum line in the various age classes (Tab. V) for the two areas further substantiates our conclusion that wear is far less rapid in Michigan deer.

Individual variation in tooth development and wear.—It is not within the scope of this paper to elaborate on the individual variation found in our known-age jaw collection. There is considerable latitude between the development and replacement of teeth in individual deer, but this variation does not affect the hunting season age determination.

The same is not true of tooth wear. Normally, careful scrutiny makes it possible to separate the 1½-year-olds with permanent premolars from the 2½-year group. But nearly a quarter of the known-age 2½-year jaws have most of the characteristics of 3½-year-old deer. Our sample of fourteen 3½-year jaws is relatively uniform. One appeared younger and at least one a year older. Nine jaws in the 4½–5½-year class were not so uniform. One 4½-year and two 5½-year deer possessed wear characteristics of 3½-year animals and one 5½-year jaw looked similar to a 6½-year-old jaw.

The five jaws in the 6½–8½ class are all reasonably consistent with the possible exception of one 6½-year specimen similar to those 4½–5½ years. A single 9½-year deer had the wear pattern of the 6½-year known-age specimens, but the two jaws 12 and 12½ years old were consistent with trends in wear.

Because of the variability found between agers on our yearly aging tests, we conducted a similar test using part of our known-age mandi-

TABLE VII

Distribution of Observed Ages on a Test of Known-Age Jaws

Known Age	No. of Jaws	Observed Age Distribution									
		1½	2½	3½	4½	5½	6½	7½	8½	9½	10½
1½	15	97%	1%		1%	1%					
2½	19	11%	69%	18%	2%						
3½	11		21%	57%	19%	2%	1%				
4½	5		5%	42%	41%	11%	1%				
5½	4		2%	19%	35%	23%	15%	4%	2%		
6½	1		3%	6%	58%	17%	8%	3%	5%		
8½	1				3%	25%	42%	16%	14%		
12½	1					6%	9%	21%	32%	15%	17%
Total	57										

bles. We told agers only that these were known-aged jaws. They were to employ the usual age criteria in making their determinations. Several jaw-boards were available for comparison. In this test, 36 individuals aged 63 jaws from 1½ to 12½-year-old deer, but we tallied responses only on 57 jaws within one month of each half-year class. Table VII compares the observed distribution with known ages. Compared to our other tests (Tab. II), there was a greater tendency to under-age 4½-year-old and older deer as we expected, but there was also a somewhat greater spread of determinations for each age.

Discussion

Now that we have seemingly cast a large shadow of doubt over the validity of our current aging standard as well as our ability to employ the technique, we need to make some adjustments in our procedures.

In order to present information derived from our known-age mandibles in the most useful form we have developed a key for separating deer killed in November into eight age classes (Appendix). Use of the key in conjunction with the accompanying plates showing a typical jaw from each age class should serve to illustrate diagnostic characteristics. This, of course, cannot wholly substitute for actual visual comparisons with known-age jaws, which we believe is the most accurate procedure. Moreover under Michigan checking station

conditions, where we have examined over 1,200 deer at one station in one day, it is not practical to attempt more time-consuming methods. These include ratios of tooth measurements, which Robinette et al. (1957) employed for mule deer, and the use of several specific characters as utilized by Quimby and Gaab (1957) in aging elk. The latter workers concluded, however, that direct comparison with known-age jaws was the best method.

We feel we should use these new standards this coming deer season. There are no conflicts involved in employing these methods for the Upper Peninsula, but we do not have an equivalent collection of jaws from the Lower Peninsula. Moreover we have shown difference in rate of tooth replacement in both fawns and yearlings between peninsulas. Our strongest support comes from the single 12½-year-old jaw from Crawford County, which fits wear sequences of Upper Peninsula deer and not New York. The other argument is simply one of spatial relationships—we assume that deer in the two parts of Michigan are more closely related than deer from the Lower Peninsula and New York.

We need to emphasize characteristics of the 2½-year, 3½-year, and 4½-year age classes in our training sessions. We should terminate attempts to classify fawns into 5-month or 6-month fawns. We should also make better use of personnel who demonstrate an aptitude for application of aging techniques.

Unless current attempts to use other methods for deer aging—such as eye lens weight—prove more exacting, we should trap and release wild deer in the Lower Peninsula or establish large enclosures in order to obtain a good sample of known-age deer jaws.

Summary

An analysis of the use of tooth replacement and wear criteria for aging white-tailed deer in Michigan indicated a disturbing lack of consistency and showed a tendency to under-age 4½-year-old and older deer and to over-age 5-month fawns, 1½ and especially 2½-year-old deer. Aging errors apparently show up in kill curves plotted from examination of a sample of the kill as a shortage of 2½-year-olds, a surplus of 3½-year-olds and older deer, and survival rates which are higher than actual. We have found differences in rate of tooth replacement in fawns and yearlings between Upper and Lower Peninsula deer.

Data from a collection of known-age mandibles indicated that our current standards based on New York deer are not accurate. Comparisons with New York data disclosed slower replacement of incisors and premolars and a much-reduced rate of wear with increasing age on cheek teeth. We present a new aging key for use in Michigan and make suggestions to improve precision of our application of the technique.

LITERATURE CITED

Anonymous. 1952. Some Facts about Michigan Deer. Mich. Dept. Cons., Game Div. Rep. 1142, 10 pp. mimeo.

Cahalane, V. H. 1932. Age Variations in the Teeth and Skull of the White-tailed Deer. Cranbrook Inst. Sci., Pub. 2, 14 pp.

Cowan, I. McT. 1936. Distribution and Variation in Deer (Genus *Odocoileus*) of the Pacific Coastal Region of North America. Calif. Fish and Game, 22: 155–246.

Eberhardt, L. L. 1958. Deer in 1958. Mich. Dept. Cons., Game Div., Information Circular 113, 24 pp. mimeo.

—— and L. D. Fay. 1957. Deer Biological Data, 1951–1956. Mich. Dept. Cons., Game Div. Rep. 2135. 67 pp. mimeo.

—— 1958. Deer Biological Data, 1957–1958. Mich. Dept. Cons., Game Div. Rep. 2192. 27 pp. mimeo.

—— 1959. Deer Biological Data, 1958–1959. Mich. Dept. Cons., Game Div. Rep. 2235. 25 pp. mimeo.

Flyger, V. F. 1958. Tooth Impressions As an Aid in the Determination of Age in Deer. J. Wildl. Mgmt., 22: 442–443.

Hamerstrom, F. N., and F. L. Camburn. 1950. Weight Relationships in the George Reserve Deer Herd. J. Mamm., 31: 5–17.

Haugen, A. O., and L. A. Davenport. 1950. Breeding Records of Whitetail Deer in the Upper Peninsula of Michigan. J. Wildl. Mgmt., 14: 290–295.

Hayne, D. W., and L. Eberhardt. 1952. Notes on the Estimation of Survival Rates from Age Distributions of Deer. Paper presented at 14th Midwest Wildl. Conf., Des Moines, Iowa, December 17–19.

Hibbard, C. W. 1951. Animal Life in Michigan During the Ice Age. Mich. Alumnus Quart. Rev., 57: 200–208.

McLean, D. D. 1936. The Replacement of Teeth in Deer As a Means of Age Determination. Calif. Fish and Game, 22: 43–44.

Park, B. C., and Besse B. Day. 1942. A Simplified Method for Determining the Condition of White-tailed Deer Herds in Relation to Available Forage. U.S.D.A. Tech. Bull. 840, 60 pp.

Peterson, R. L. 1955. North American Moose. (Appendix A—A study of mandibular tooth-wear as an index to age of moose by R. C. Passmore, R. L. Peterson, and A. T. Cringan). U. of Toronto Press, 280 pp.

Pope, G. W. 1934. Determining the Age of Farm Animals by Their Teeth. U.S.D.A. Farmers Bulletin No. 1721, 13 pp.

Quimby, D. C., and T. E. Gaab. 1957. Mandibular Dentition As an Age Indicator in Rocky Mountain Elk. J. Wildl. Mgmt., 21: 435–451.

Ricker, W. E. 1948. Methods of Estimating Vital Statistics of Fish Populations. Indiana University Publ., Science Series No. 15. 101 pp.

Riney, T. 1951. Standard Terminology for Deer Teeth. J. Wildl. Mgmt., 15: 99–101.

Robinette, W. L., D. A. Jones, G. Rogers, and J. S. Gashwiler. 1957. Notes on Tooth Development and Wear for Rocky Mountain Mule Deer. J. Wildl. Mgmt., 21: 134–153.

Severinghaus, C. W. 1949. Tooth Development and Wear As Criteria of Age in White-tailed Deer. J. Wildl. Mgmt., 13: 195–216.

—— and E. L. Cheatum. 1956. Life and Times of the White-tailed Deer, pp. 57–186, *in* The Deer of North America, ed. by W. P. Taylor, Harrisburg, Penn., Stackpole Co., 668 pp.

—— and J. E. Tanck. 1950. Condition of the Mandibular Teeth of a Sixteen and a Half Year Old White-tailed Deer. J. Wildl. Mgmt., 14: 382–384.

APPENDIX

Key to the Age of Michigan Deer in November

(Based on Known-Age Dentition)

1. a) Temporary incisors entire or possibly center ones replaced by larger permanent teeth. First molar present, but rarely the second.—Fawns, 5–6 months old, Fig. 4.
   b) All permanent incisors present, Fig. 4. Third molar erupted, although posterior cusp may not be visible.—1½ years old or older.—2.
2. a) Temporary premolars present (fourth premolar 3-parted), Fig. 5, or permanent premolars replacing temporary ones.—1½ years old.
   b) All permanent premolars in position and fully erupted (fourth premolar 2-parted).—1½ years or older.—3.
3. a) No wear on permanent premolars. Posterior cusp of third molar generally not erupted. Little or no wear on crests of third molar and dentine, if showing, in a narrow line.—1½ years old, Fig. 6.
   b) Greater wear indicated, last crest of third molar erupted.—2½ years or older.—4.
4. a) Wear absent or very slight on third premolar; slight on fourth, usually with only slight amounts of dentine showing on anterior surface. Lingual crests of all molars usually sharp, dentine line very narrow on third molar. Slight wear on last cusp of third molar.—2½ years old, Fig. 7.
   b) Wear further advanced.—3½ years or older.—5.
5. a) Last cusp of third molar flattened, hollowed-out or both. Third premolar with thin to moderate dentine line on anterior surface. Lingual crest of first molar blunt. Lingual crests of other molars sharp.—3½ years old, Fig. 8.
   b) Further wear indicated.—4½ years or older. It is difficult to determine the age accurately above 3½ years due to individual variation in tooth wear. However, certain wear characteristics are found in most jaws of each age group.

Characteristics are listed below:

4½–5½ years old: Lingual crests of first molar present but flat. Crests of second molar rounded as first molar in 3½-year group. Posterior cusp of third molar may be worn so it slopes laterally downward. Third and fourth premolars further worn. Second premolar may or may not show wear, Figs. 9 and 10.

6½–8½ years old: Fourth premolar and first molar usually flat, lingual crests of second molar sometimes missing, especially at upper age limits. Third molar retains lingual crests at all stages, Figs. 11 and 12.

9½–12½ years old: Wear on mandibular cheek teeth greater than above, but in no instance are all teeth flat. Usually there is evidence of lingual crests remaining, at least on the third molar. Extreme variation in wear may occur, especially in the fourth premolar and first molar. Presence or absence of incisors not a valid criterion of this age group, since known-age specimens and several deer known to be older all retained incisor teeth in good condition, Fig. 13.

Old age: No lingual crests present. Molar teeth frequently hollowed-out or entirely flat. Teeth may be missing or show extremely uneven wear, and some shrinking away of bone around roots of teeth may have occurred, Fig. 14.

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SEASONAL MORTALITY AND GROWTH OF HATCHERY-REARED BROOK AND RAINBOW TROUT IN EAST FISH LAKE, MONTMORENCY COUNTY, MICHIGAN, 1958–59

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Introduction

More knowledge must be gained about trout populations if suitable stocks of trout are to be maintained for the angling public. Two characteristics of fish populations that are of primary importance are mortality and growth. Many studies have been made of the growth of trout but considerably fewer on mortality, or its complement, survival. Most published data on mortality (as well as growth) pertain to relatively long intervals, compiled on an annual basis. Seasonal mortality patterns and factors affecting this mortality for various types of trout populations and environments need to be determined. Similar information on trout growth is highly desirable.

The present study considers seasonal mortality and growth between October, 1958, and September, 1959, of hatchery-reared brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) released in East Fish Lake, Montmorency County.

East Fish Lake has a surface area of 16 acres. More than half of the basin is deeper than 20 feet and the maximum depth is about 40 feet. It stratifies in midsummer, but oxygen and temperature levels are suitable for trout throughout the year. The water is hard (about 175 p.p.m. of methyl-orange alkalinity). Aquatic vegetation is sparse except on the shoals, where *Chara* is common and scattered patches of *Scirpus* spp., *Potamogeton* spp., and *Nuphar* spp. occur. Brook sticklebacks (*Eucalia inconstans*) and mudminnows (*Umbra limi*) are the only species of fish other than trout which have been

observed since the fall of 1956, when the lake was treated with rotenone.

East Fish Lake is an ideal body of water for the type of study discussed here. It has a reputation of being excellent brook trout water and is situated on the Hunt Creek Trout Research Area, where a fishing-permit system ensures a complete creel census. Also, the lake has a barrier weir at the outlet, which isolates the trout population.

We wish to thank O. M. Corbett, A. M. Schiffman, G. D. Betts, and T. H. Turppa of the Hunt Creek Trout Research Station for their assistance in the collection of the data for this study.

Methods

Hatchery-reared brook and rainbow trout of identical length and age (1) were used so that survival and growth of the two species could be compared. On October 14, 1958, 300 brook and 300 rainbow trout ranging in total length from 8.5 to 9.5 inches (average, 8.9) were marked by removal of the left pelvic fins and planted in East Fish Lake.

Population estimates and growth data were obtained from these populations of trout during the following periods (which are discussed consecutively in the text): October 14–November 6; November 6–12; December 29–January 9; February 26–March 11; April 20–22; and the winter of 1959–60. All population estimates were regarded as applying to the midpoint date of each of these periods. Estimates for rainbow trout were made only for January 2, March 4, and the winter of 1959–60 because too few fish were marked in other periods to permit satisfactory estimates.

Four different estimates were obtained (based on different methods of recovery) of the number of brook trout present in East Fish Lake during the first period (October 14–November 6). All four estimates were based on recaptures from 150 different brook trout trap-netted and marked during this period. Trout were removed from the nets daily and returned to the lake after the lower parts of the caudal fins had been removed. All estimates for this first period, and for later periods, were based on the numbers of marked and unmarked trout among fish recovered, and it was assumed throughout the study that the mortality rates of the marked and unmarked members of the population were identical. The first population estimate was based on recapture by netting during the netting period; the second on recap-

ture by experimental fishing on November 6–12; the third on recapture by direct-current electrofishing on April 20–22; and the fourth on recoveries by anglers during the 1959 fishing season (April 25–September 13). The first two population estimates were made by the method suggested by Schumacher and Eschmeyer (1943), and the latter two (and other estimates discussed below) were based on the Petersen Index.

During the second period (November 6–12), or the period of fall experimental angling, 95 different brook trout were caught by angling with artificial flies or salmon eggs. These trout were marked by clipping the dorsal lobes of the caudal fins. Two estimates were obtained of the brook trout population for the second period—one from the number of upper-caudal-marked trout and unmarked fish in the sample taken by spring electrofishing and the other from the number of marked and unmarked trout in anglers' creels during the trout season.

Between December 29 and January 9, 38 brook and 49 rainbow trout were caught by angling through the ice. These trout were marked by removing the right pectoral fins before returning them to the water. Petersen-type population estimates for this period were based on the ratio of these marked trout observed among fish collected in the spring electrofishing and in the anglers' catch during the season.

Ice fishing was again employed to capture trout between February 26 and March 11. A total of 52 brook and 46 rainbow trout were caught and marked by removing the right pelvic fins. Population estimates for this fourth period were calculated from the ratios of marked to unmarked trout in the spring electrofishing and in the anglers' catch.

On April 20–22, just prior to the trout season, 42 brook trout were captured by direct-current electrofishing. These fish were marked by removing the dorsal fins. Population estimates for the period were based on the ratio of dorsal-marked to unmarked trout in the anglers' catch.

No direct population estimates utilizing the mark-and-recapture method were attempted during the 1959 trout season. The numbers of trout caught by fishermen, however, were shown by the creel census. The total catch subtracted from the preseason population estimate gave a hypothetical fall population remaining after the season.

Also, the anglers' catch for various 2-week intervals during the angling season gave us some indication of the mortality pattern during the trout season.

Population estimates were not conducted in the fall of 1959. However, a fair knowledge of the population of trout remaining after the fishing season was gained by experimental ice fishing in the winter of 1959–60.

Results

The population estimates for different dates from October 26 to April 21 are shown in Table I. As mentioned above, four estimates were made, all based on trap-netted fish but on different methods of recovery, for October 26 (midpoint of the October 14–November 6 period). The four estimates were 329, 285, 300, and 314.[1] The first two estimates were determined by the Schumacher-Eschmeyer method; one was based on trout recovered by netting and the other on recoveries by experimental angling. The third was a Petersen estimate based on marked and unmarked trout recovered during spring electrofishing; and the fourth was based on fish creeled by anglers during the season.

The estimates of the number of brook trout in East Fish Lake on November 9 (the midpoint of the November 6–12 marking period) were 285 (based on 14 fin-clipped trout out of 42 brook trout captured by spring electrofishing) and 288 (on the basis of the ratio of marked to unmarked trout creeled during the fishing season). A comparison of these estimates with estimates for October 26 suggests that about 13 brook trout died between the two dates.

Recaptures by electrofishing of trout marked on December 29–January 9 yielded a population estimate of 123 brook trout for January 2; recoveries by anglers gave an estimate of 124. Thirty-two marked rainbow trout among 197 creeled during the fishing season gave an estimated population of 302 for January 2. (Too few rainbow trout were captured by spring electrofishing to make a second estimate.) These data suggest that the rainbow trout suffered little mortality between planting and early January, whereas the brook trout

[1] These early estimates of the population soon after the planting date demonstrated that the methods used in determining population numbers were reliable because the estimates were close to the actual numbers known to have been planted.

TABLE I

ESTIMATES OF THE POPULATION OF BROOK AND RAINBOW TROUT IN EAST FISH LAKE, OCTOBER 26, 1958, TO APRIL 21, 1959

Species and Date[1] of Estimate	Type of Estimate[2]	Method of Original Capture[3]	Method of Recapture[3]	Number of Fish Marked	Number of Marked Fish Recovered	Number of Unmarked Fish Recovered	Population Estimate[4]
Brook trout							
Oct. 26, 1958	S	N	N	150	—	—	329 (243–415)
	S	N	A		—	—	285 (239–331)
	P	N	E		21	21	300 (224–469)
	P	N	C		42	46	314 (246–405)
Nov. 9, 1958	P	A	E	95	14	28	285 (183–475)
	P	A	C		29	59	288 (202–396)
Jan. 2, 1959	P	A	E	38	13	29	123 (81–224)
	P	A	C		27	61	124 (90–181)
Mar. 4, 1959	P	A	E	52	22	20	99 (83–123)
	P	A	C		43	45	106 (85–137)
Apr. 21, 1959	P	E	C	42	36	52	103 (79–145)
Rainbow trout							
Jan. 2, 1959	P	A	C	49	32	165	302 (213–445)
Mar. 4, 1959	P	A	C	46	31	166	292 (200–418)

[1] Midpoint of period during which trout were captured for marking.

[2] S = Schumacher and Eschmeyer; P = Petersen.

[3] N = trap netting; A = experimental angling; E = electrofishing; C = public fishing during the trout season.

[4] 95 per cent confidence limits in parentheses.

population estimate of 124 suggests a mortality of about 163 between November 9 and January 2 (or a total of 176 out of 300 since the date of planting).

The occurrence of 22 fish which had been marked on February 26–March 11 among 42 brook trout captured in the spring electrofishing gave a population estimate of 99 brook trout as of March 4,

1959; the ratio of 43 marked trout out of 88 in the anglers' catch yielded an estimate of 106 (average of the two estimates, 103). This indicated a mortality of about 21 brook trout (17 per cent of the number remaining in early January) between January 2 and March 4. The rainbow trout population of 292 on March 4 was calculated from 31 right-pelvic-marked trout among 197 caught by anglers.

The brook-trout population estimate for April 21 was based on recoveries from 42 brook trout captured by electrofishing and marked by clipping the dorsal fins. The 36 marked fish recorded among 88 brook trout creeled during the fishing season gave an estimate of 103. Assuming that little or no mortality occurred among the rainbow trout between March 4 and April 21, about 292 rainbow and 103 brook trout were present at the opening of the trout season.

No direct population estimates were made during the 1959 angling season, but the complete creel census provided data on fish caught as the season progressed. These data, divided according to successive 2-week intervals of the trout season (Tab. II), were combined with data from the earlier population studies to provide the logarithmic curve of mortality in Fig. 1. Of the estimated 103 brook trout present at the opening of the fishing season, anglers caught 52 during the first 2 weeks of the season, 30 during the second 2 weeks, and 6 during the remaining 16 weeks. Subtracting the total catch of 88 from the population estimate of April 21 leaves only 15 brook trout whose fate was unknown. Thus we believe that the brook trout mortality curve of Fig. 1 is closely representative of mortality during the year.

Rainbow trout were caught by anglers at a much slower rate than brook trout. Of the 292 available to anglers at the opening of trout season, 44 were creeled during the first 2-week period of the fishing season and 33 during the second (Tab. II). Subsequent catches were smaller, but as many as 17 were caught during the last 2 weeks of the season. The total catch was 197, which left 95 rainbow trout unaccounted for at the close of the season. Experimental fishing in December 1959 and January and March 1960 yielded 13 rainbow trout (no brook trout) from the October 1958 planting. Our only estimate of the number of rainbow trout remaining in the lake was based on the recovery of 1 marked trout among the 13 taken. We had marked 3 rainbow trout in October 1959 by electrofishing, so that the estimate of rainbow trout surviving the trout season (based on these limited data) was 39. Thus a maximum of 82 (as few as 56, if the population

TABLE II

MORTALITY ESTIMATES FOR BROOK AND RAINBOW TROUT IN EAST FISH LAKE, OCTOBER 14, 1958, TO SEPTEMBER 13, 1959

Period	Days in Period	Brook Trout			Rainbow Trout		
		Mortality during period[1]	Estimated number of fish surviving	Instantaneous mortality rate per day	Mortality during period[1]	Estimated number of fish surviving	Instantaneous mortality rate per day
Oct. 14–Oct. 26	12	0	300	0	0	300	0
Oct. 27–Nov. 9	14	13	287	0.00314	0	300	0
Nov. 10–Jan. 2	54	163	124	0.01554	0	300	0
Jan. 3–Mar. 4	61	21	103	0.00303	8	292	0.00045
Mar. 5–Apr. 21	48	0	103	0	0	292	0
Apr. 22–May 8	17	52	51	0.04136	44	248	0.00963
May 9–May 22	14	30	21	0.06334	33	215	0.01019
May 23–June 5	14	3	18	0.01102	16	199	0.00549
June 6–June 19	14	0	18	0	30	169	0.01169
June 20–July 3	14	1	17	0.00412	38	131	0.01821
July 4–July 17	14	0	17	0	7	124	0.00389
July 18–July 31	14	0	17	0	1	123	0.00057
Aug. 1–Aug. 14	14	1	16	0.00434	7	116	0.00419
Aug. 15–Aug. 28	14	0	16	0	4	112	0.00247
Aug. 29–Sept. 13	16	1	15	0.00400	17	95	0.01178

[1] Mortality during periods prior to April 22 is based on population studies and for subsequent periods on observed fishing mortality.

estimate is accepted) rainbow trout died of natural causes during the fishing season.

DISCUSSION OF MORTALITY

The instantaneous rate of mortality (Ricker, 1958) of brook trout was greatest during the first 4 weeks of the trout season (Fig. 1) but nearly all of this was fishing mortality (82 trout caught). From November 9 to January 2 the rate was somewhat less, but the numerical loss or total mortality (163) was far greater, and it is assumed that all these trout fell prey to natural causes. Thus two-thirds of the brook trout planted had died before the fishing season opened. Anglers caught 88 of 103 (85 per cent) of the brook trout available

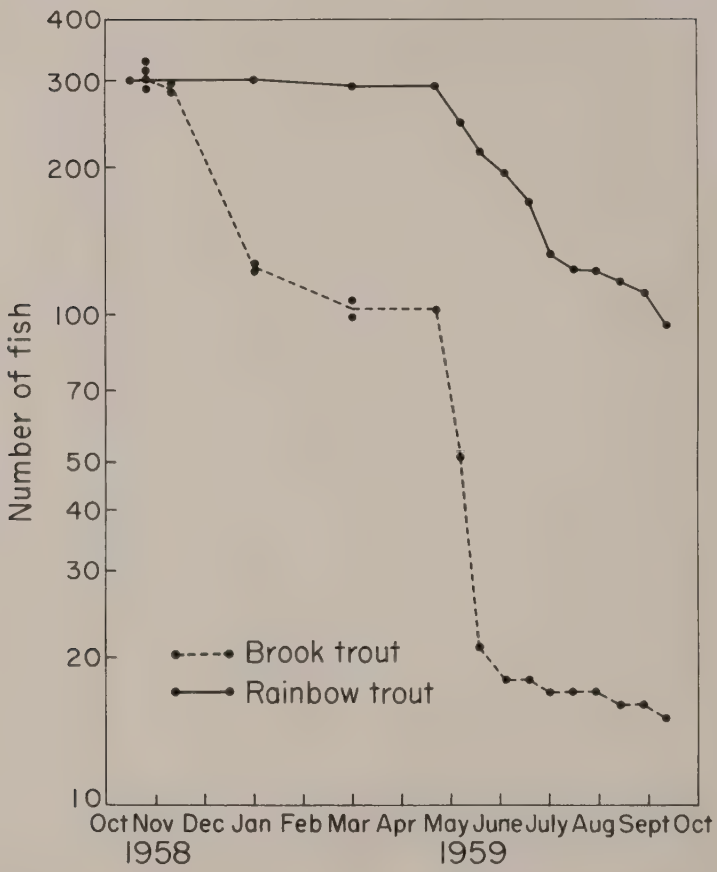

FIG. 1. Estimated populations of brook and rainbow trout plotted on logarithmic scale, showing seasonal instantaneous mortality rates.

at the opening of the trout season, but this was only 29 per cent of the number planted at the beginning of the study.[2]

[2] Anglers caught 82 per cent of 350 hatchery-reared brook trout planted in East Fish Lake immediately before the trout season in 1957 (92 per cent of the catch was made during the first 4 weeks of the season). The similarity in the

Both the natural and fishing mortality rates of rainbow trout were very different from those of brook trout. It was estimated that only 8 rainbow trout died between planting and the opening of the trout season. Anglers caught 197 of 292 (67 per cent) of the rainbow trout available at the opening of the season, or 65 per cent of the number planted. The catch of rainbow trout was distributed throughout the entire season, whereas 93 per cent of the total brook trout catch was made during the first 4 weeks of the fishing season (Tab. II).

Growth

The total length of all trout handled during each phase of this study, and both lengths and weights of all trout caught by anglers during the fishing season, were recorded. A summary of the average lengths and weights, with the standard errors, are presented in Table III.

The average length of both species of trout at planting in October was 8.9 inches. By January brook trout had gained an average of 1.0 inches, where rainbow trout had gained 1.7 inches. The "t" test showed that by this date rainbow trout were significantly longer than brook trout; they maintained this advantage throughout the study. Brook trout caught during the first 2 weeks of the trout season averaged 10.9 inches in length, whereas rainbow trout were 11.5 inches long. The length of one brook trout creeled during the last 2 weeks of the season was 14.1 inches, whereas 17 rainbow trout averaged 16.3 inches; thus the average increment between October 14, 1958, and the end of the 1959 trout season was 5.2 inches for brook trout and 7.4 inches for rainbow trout.

Growth in weight of brook and rainbow trout, in general, followed a similar seasonal pattern (Fig. 2). Between October 14 and January 2, increase in weight (calculated from a length-weight curve) was rapid; brook trout gained 52 per cent of their weight at planting and rainbow trout gained 83 per cent. The instantaneous rate of growth (Ricker, 1958) of rainbow trout was 44 per cent faster than brook trout. It was during this period in late fall and early winter that rainbow trout gained the advantage that they held throughout the rest of the study. Growth was negligible from January 2 to April 21, but in-

known exploitation rate of 1957 and the estimated exploitation rate in the present study supports the reliability of the population estimate of 103 brook trout prior to the 1959 trout season.

TABLE III

AVERAGE LENGTH AND WEIGHT OF BROOK AND RAINBOW TROUT ON VARIOUS DATES, EAST FISH LAKE, OCTOBER 14, 1958, TO SEPTEMBER 5, 1959

Date	Brook Trout				Rainbow Trout			
	Number of fish	Average total length (inches)[1]		Average weight (pounds)[1,2]	Number of fish	Average total length (inches)[1]		Average weight (pounds)[1,2]
Oct. 14	300	8.90	(0.018)	0.25	300	8.90	(0.018)	0.23
Jan. 2	38	9.88	(0.095)	0.38	49	10.57	(0.066)	0.42
March 4	54	10.21	(0.062)	0.41	46	10.72	(0.072)	0.44
April 21	42	10.53	(0.077)	0.45	9	11.02	(0.316)	0.48
May 1	52	10.85	(0.059)	0.48 (0.010)	44	11.53	(0.069)	0.56 (0.010)
May 15	30	10.97	(0.098)	0.53 (0.018)	33	11.85	(0.101)	0.64 (0.015)
May 29	3	10.90	(0.485)	0.53 (0.015)	16	12.43	(0.110)	0.76 (0.023)
June 12	—	—		—	30	13.48	(0.125)	1.00 (0.025)
June 26	1	11.50		0.70	38	13.79	(0.101)	1.09 (0.028)
July 10	—	—		—	7	14.17	(0.286)	1.16 (0.063)
July 24	—	—		—	1	15.00		1.25
Aug. 7	1	13.50		1.22	7	15.94	(0.193)	1.64 (0.064)
Aug. 21	—	—		—	4	16.38	(0.144)	1.79 (0.032)
Sept. 5	1	14.10		1.31	17	16.34	(0.129)	1.78 (0.033)

[1] Standard errors in parentheses.

[2] Weights for both species for January 2, March 4, and April 21 determined from length-weight-relationship table.

creased markedly after this date (Fig. 2). Both species grew at a fairly constant instantaneous rate from late April to September, with brook trout growing at a somewhat slower rate. There apparently was a slight slowdown during midsummer in the rate of growth of rainbow trout, but the samples were not large enough to be certain.

Rainbow trout gained an average of 0.25 pound from October 14 to April 21 and an additional 1.30 pounds by September 13. The increment in weight of rainbow trout for the study period was 1.55 pounds (520 per cent). Brook trout gained an average of 0.20 pound from October 14 to April 21 and the 2 brook trout creeled late in the trout season (1 in August, 1 in September) had gained an additional 0.82 pound (average); the weight increment since planting was 1.02 pounds, or 408 per cent.

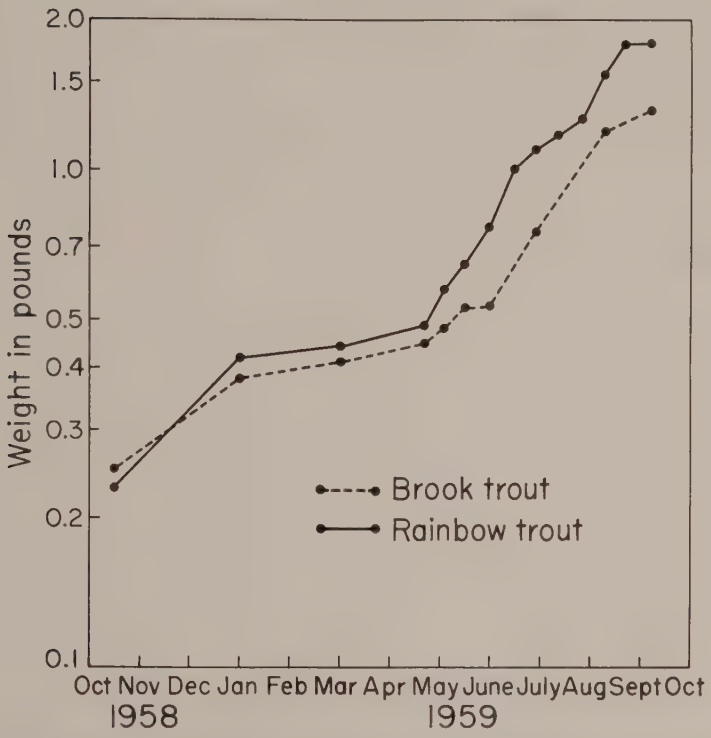

FIG. 2. Weight of brook and rainbow trout plotted on logarithmic scale showing seasonal instantaneous growth rates.

DISCUSSION

Because of the higher survival and faster rate of growth, the return of rainbow trout to anglers was much better than brook trout (a few additional recaptures of rainbow trout are expected during the 1960 fishing season). This was the first introduction of rainbow trout into East Fish Lake, however, whereas brook trout have been planted annually for many years. It is widely acknowledged that initial introductions of trout in suitable lakes usually fare better than later plantings. We expect to obtain additional information on this point from similar future plantings in East Fish Lake and other waters.

The poor return of brook trout was due primarily to low survival between November 9 and January 2. The causes of this mortality are unknown. Since we know when the mortality occurred, however, certain possibilities (e.g., planting mortality) may logically be eliminated. It was observed during the fall netting and fishing that brook trout were in shallow water, whereas rainbow trout stayed in the deeper water. Brook trout could be seen and approached easily by rowboat during late October and early November, a period which coincides with the brook trout spawning season and the period of heavy mortality. Around November 9, 1958, most of the female brook trout captured were ripe, but had not yet spawned. The concentration of brook trout on the inlet delta and vicinity during this period may have encouraged predation by kingfishers, herons, mink, and otter, all of which are known to frequent the area and presumably can capture trout in shallow water. Another possibility is furunculosis, a disease which may cause death at this time of year because the physical resistance of the brook trout is lowered due to spawning. Still another possibility might be that the trout died from a physiological change associated with spawning. (Hatchery brook trout of this age and size that are held in hatchery ponds are known to suffer mortality at the same time of year.) Although the heavy brook trout mortality of November 9–January 2 remains unexplained, these and other possibilities suggest potentially productive avenues for future research on the problem.

LITERATURE CITED

Ricker, W. E. 1958. Handbook of Computations for Biological Statistics of Fish Populations. Bull. Fish. Res. Bd. Canada, 119: 300 pp.

Schumacher, F. X., and R. W. Eschmeyer. 1943. The Estimate of Fish Population in Lakes or Ponds. Jour. Tenn. Acad. Sci., 18(3): 228–249.

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ZOOLOGY

LATE CENOZOIC CYPRINID FISHES FROM IDAHO WITH NOTES ON OTHER FOSSIL MINNOWS IN NORTH AMERICA

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The oldest known fossil record for a cyprinid fish in North America is from the Miocene of British Columbia. It is reasonable to assume that cyprinids migrated from Asia by way of a Bering land bridge during the long Miocene epoch. At that time, a temperate climate is supposed to have existed in the northern part of the North American and Eurasian continents (Dorf, 1959)—a condition suitable for cyprinid migration.

The paleontological study of cyprinid fishes in North America has been meager because of the lack of an adequate knowledge of the comparative osteology of Recent forms (Miller, 1959, p. 194). Since Cope's time comparatively few fossil cyprinids have been reported, and the earlier ones usually have been incorrectly placed generically. Consequently a revision of the known fossil minnows is desirable. But without detailed osteological knowledge of modern cyprinids, adequate systematic studies of the fossil faunas is impossible, and the description of new fossil species only adds confusion to an already chaotic situation.

In the present study I describe the cyprinids found associated with other fossils in the Late Cenozoic beds in Idaho. I have also commented on the previously described fossil minnows in North America, including some proposals for new generic arrangement.

The fossil cyprinids described in this report were collected by Dwight W. Taylor in the summers of 1955, 1956, and 1957 and C. W. Hibbard in the summer of 1956. The mammalian faunas from most of the localities cited have been described by Hibbard (1959), a small part of the molluscan fauna has been identified by Taylor (Hibbard, 1959), and the fish fauna exclusive of the Cyprinidae is being studied by Carter Gilbert.

All fossils were collected by surface picking. Representatives of the living relatives which were compared with the fossils are deposited in the University of Michigan Museum of Zoology. The fossils are deposited in the United States National Museum (USNM) and the University of Michigan Museum of Paleontology (UMMP).

List of Localities

All locality numbers are in the U.S. Geological Survey (USGS) Cenozoic Series, and field numbers are in parentheses.

Unnamed local fauna.—Middle Pliocene, Brown formation. Locality 20095 (DWT T56-52). Owyhee Co., Idaho. Oreana quad. (1950) 1:24000. NE. ¼ Sec. 12, T. 5 S., R. 1 W. 2000'S., 750' W. of NE. corner. Fossils from tuffaceous silt (many in nodules), in amphitheater at head of small gully. Data furnished by Dwight W. Taylor.

Sand Point local fauna.—Late Pliocene, unnamed formation (Yen, 1944; Hibbard, 1959). This fauna is known from the following localities:

19128 (DWT 406). Owyhee Co., Idaho. Hammett quad. (1948) 1:24000. SW. ¼ Sec. 1, T. 6 S., R. 8 E. 650'–1050' N. of SW. corner. 2600' elev. Abundant shells and fewer of other fossils weathering from fine sand. Most if not all fossils are from a sandy coquina about 6" thick.

19129 (DWT 407). Owyhee Co., Idaho. Hammett quad. SW. ¼ Sec. 1, T. 6 S., R. 8 E. 1950' E., 950' N. to 2200' E., 525' N. of SW. corner. 2690' elev. Fossils from a 15'–20' interval of tan, fine, cross-bedded sand immediately above a 2'–3' thick ash bed. This is probably very close to the locality from which Yen (1944) described freshwater mollusks.

Unnamed local fauna.—Probably equivalent to the Sand Point local fauna: Late Pliocene from an unnamed formation. Data furnished by Dwight W. Taylor.

20475 (T57-50; FIC-152). Elmore Co., Idaho. Indian Cove quad. (1948) 1:24000. SW. ¼ Sec. 16, T. 5 S., R. 8 E. 1550'–1650' E., 1300'–1450' N. of SW. corner. 2730' elev. Fine sand exposed in borrow pit for abandoned railroad right-of-way.

20195 (T56-96). Elmore Co., Idaho. 1650' W., 1700' N. of SE. corner. Sec. 5, 7 S., 3 E. Oolite capping bluffs.

Hagerman local fauna.—Early Pleistocene (probably Aftonian). Hagerman Lake Beds (H. T. Stearns 1932) = Hagerman formation (C. W. Hibbard 1959). Following locality data furnished by C. W. Hibbard and D. W. Taylor:

19194 (DWT 429). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. NE. ¼ Sec. 20, T. 7 S., R. 13 E. 350' W., 875' S. to 50' W., 850' S. of NE. corner. 3100' elev. Shells from south side of an E-W trending ridge, from 5' tan silt, massive, weathering buff; lowest such light-colored bed in section.

19213 (DWT 427). Twin Falls Co., Idaho, Hagerman quad. (1950) 1:24000. NW. ¼ Sec. 21, T. 7 S., R. 13 E. 700' E., 100' S. to 1150' E., 400' S. of NW. corner. 3097' elev. Fossils from a 6' bed of tan silt weathering nearly white, the lowest light-colored bed exposed in the gulch.

19216 (DWT 431). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000.

NE. ¼ Sec. 20, T. 7 S., R. 13 E. 1100′ W., 775′ S. to 1150′ W., 650′ S. of NE. corner. 3295′ elev. 25′ below gravel. Fossils from fine, micaceous, cross-bedded, gray sand.

19217 (DWT 432). Twin Falls Co., Idaho. Hagerman quad. NE. ¼ Sec. 20, T. 7 S., R. 13 E. 150′ W., 800′ S. of NE. corner. 3115′ elev., 205′ below gravel. Fossils from fine sand and silt exposed on bench on ridge.

19221 (DWT 443). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. SW. ¼ Sec. 16, T. 7 S., R. 13 E. 700′ E., 750′ N. of SW. corner. 3110′ elev. 3′ bed of tan silt, weathering buff: lowest prominent light-colored bed in section.

20128 (DWT 413). Elmore Co., Idaho. Ticeska quad. (1949) 1:24000. NW. ¼ Sec. 18, T. 6 S., R. 12 E. 1850′ E., 2800′ S. of NW. corner. 3100′ elev. Shells from sand and clay exposed in borrow pit 2′–5′ below top of formation.

20765 (DWT 540). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. SW. ¼ Sec. 28, T. 7 S., R. 13 E. 300′–400′ E. 2100′ N. of SW. corner. 3025′ elev. Fossils from higher saddle on south spur of square-nosed butte, from 2′–10′ above a conspicuous light gray platy-weathering 2″-thick carbonaceous clay shale. Clay shale is 20′ above upper pumice.

20987 (T56-54). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. NW. ¼ Sec. 16, T. 7 S., R. 13 E. 1300′ E., 575′ S. of NW. corner. 3300′ elev. Shells from olive clay about 10′ above floor of western of two mammal quarries and 15′ below top of formation.

21011 (FPV-92; T56-92). Elmore Co., Idaho. Ticeska quad. (1949) 1:24000. NE. ¼ Sec. 13, T. 6 S., R. 11 E. 2300′ W., 2450′ S. of NE. corner. 3040′ elev. Fossils from light gray (white-weathering) carbonaceous clay shale with abundant shells. Exposure on east side of small gully on south side of Snake River canyon. About 30′ above basalt.

21012 (T56-55). Gooding Co., Idaho. Ticeska quad. (1949) 1:2400. SW. ¼ Sec. 30, T. 5 S., R. 12 E., 250′ E., 25′ N. of SW. corner. 3075′ elev. Shells from carbonaceous papery clay shale in which thick lime ledges are developed. Fossils from the less limey clay between and below ledges.

21017 (FGF-166). Elmore Co., Idaho. Hammett quad. (1948) 1:24000. SE. ¼ Sec. 5, T. 6 S., R. 9 E. 700′ W., 1600′ N. of SE. corner. 2810′ elev. Clay just below basaltic colluvium and gravel at base of Pasadena Valley formation.

21048 (T56-48). Elmore Co., Idaho. Hammett quad. (1948). 1:24000. SE. ¼ Sec. 5, T. 6 S., R. 9 E. 1800′ N., 4175′ E. of SW. corner. 2800′ elev. Fossils from lower 2″ of a 6″-thick maroon carbonaceous papery clay shale about 12′ above bed of wash. This is the lower of two prominent maroon clay shales exposed on the north side of the wash.

21049 (T56-44). Elmore Co., Idaho. Hammett quad. (1948) 1:24000. NE. ¼ Sec. 24, T. 5 S., R. 8 E. 2250′ S., 1050′ W. of NE. corner. 2800′ elev. Road cut exposure at bottom of Hammett Grade, on Hammett-Anderson Dam road. Fossils from a 6″ light gray clay shale, weathering into almost paper-thin flakes. Five feet above a maroon carbonaceous papery clay shale, the lowest exposed bed of the formation.

21058 (FPV-19). Gooding Co., Idaho. Ticeska quad. (1949) 1:24000. NE. ¼ Sec. 7, T. 6 S., R. 12 E. 850′ W., 1400′ S. of NE. corner. Thin-bedded silt and sand 1′ above basalt exposed on road to Bliss Dam.

Grand View local fauna.—Middle Pleistocene, unnamed formation. (R. W. Wilson, 1933).

20764 (T56-39). Owyhee Co., Idaho. Jackass Butte quad. (1948). 1:24000. NE. ¼ Sec. 15, T. 4 S., R. 2 E. 1925′ W., 1950′ S. of NE. corner. 2515′ elev. Fossils from fine sand exposed on minor bench immediately south of gulch heading on E. side Jackass Butte. This is believed to be the type locality of the microtines described by Wilson.

Nomenclature and Measurement of the Pharyngeal

Since the most important part of the fossil collection consists of pharyngeals, and because many fossil cyprinids have already been described from the pharyngeals, precise definitions of the various parts of these bones are necessary (Fig. 1). The nomenclature used is mostly adopted from Chu (1935), with modifications and additions. Letters in parentheses are abbreviations used in the figures.

Length of pharyngeal (*L*) is the distance from the anterior tip to the hindmost point of the bone.

Width of pharyngeal (*W*) is a measurement of the widest dorsolateral area, from the outermost margin of the pitted surface to the nearest point on the inner margin.

Pitted surface (*P*) is the dorsolateral area easily recognizable by the presence of bony partitions, cavities or pits, and grooves.

Dentigerous surface is the area which bears the teeth.

Ventral surface (*V*) is the ventral part of the bone between the outermost edge and dentigerous surface, which affords a wide surface for the attachment of muscles.

Anterior limb (*1–2*) is the whole anteroventral portion of the pharyngeal; its length is measured from the anterior tip to the anterior angle of the bone.

Posterior limb (*2–4*) is the whole part of the pharyngeal, which is turned dorsally so as to form a gateway to the oesophagus. Its length is measured from the anterior angle to the posteromesial end of the bone.

Anterior angle (*2*) is the angle between the anterior and posterior limbs and serves as an easily recognized boundary between the two limbs.

Posterior angle (*3*) is the angle at the distal part of the posterior limb, situated where the posterior limb bends obliquely cephalad.

Anterior edentulous process (*1–5*) is the distal toothless part of the anterior limb. Its length is measured from the anterior tip to the beginning of the first tooth.

Posterior edentulous process (*4–8*) is the distal toothless part of the posterior limb, which is directed dorsad. Its length is measured from the posterior end of the base of the dentigerous surface, to the posterior tip.

Major tooth row (*6*) comprises the teeth in a row near the ventral surface of the pharyngeal. These teeth are larger and stouter than those in the minor row.

Letters I, II, III, IV, and V, are used to indicate a tooth, from posterior to anterior.

Minor tooth row (7) comprises teeth in a row near the inner margin of the pitted surface and are smaller and fewer than those in the major row. Letters (1), (2), are used for these teeth, from posterior to anterior.

Head of tooth is the upper part of a tooth above the slight constriction, and bears a hooked tip and grinding surface, if present.

Stem of tooth is the middle part of a tooth between the head and the base. This part is usually the narrowest, but it is not always conspicuously set off from the head and the base.

Base of tooth is the lower part of the tooth by which it attaches to the pharyngeal. When a tooth is replaced, the old one separates from this base and the new one grows down and fuses with it.

Relative width is the ratio of the pharyngeal width to its length.

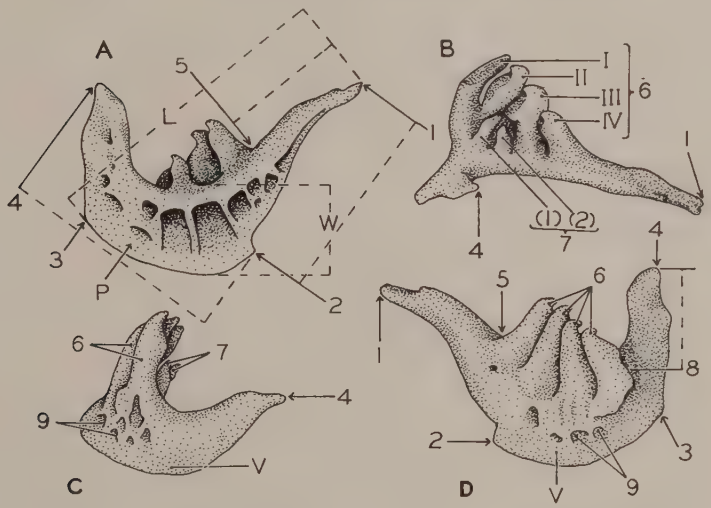

FIG. 1. The pharyngeal of *Gila atraria* (Girard) showing the nomenclature and measurements. *A*, dorsolateral view; *B*, dorsomesial view; *C*, posterior view; *D*, ventromesial view. Abbreviations: *L*, length of pharyngeal; *P*, pitted surface; *W*, width of pharyngeal; *V*, ventral surface; **1**, tip of anterior limb; **2**, anterior angle; **3**, posterior angle; **4**, tip of posterior limb; **5**, origin of major tooth row; **6**, major tooth row; **7**, minor tooth row; **8**, end of major tooth row; **9**, foramina; **1–2**, length of anterior limb; **2–4**, length of posterior limb; **1–5**, length of anterior edentulous process; **4–8**, length of posterior edentulous process.

Description and Discussion of Fossils

Mylocyprinus robustus Leidy

Mylocyprinus robustus Leidy, 1870, Proc. Acad. Nat. Sci. Phila., p. 70.

Referred materials: USGS loc. 20095. A large almost complete pharyngeal from Middle Phocene of Owyhee County, Idaho; USNM 22306. USGS loc. 19128. Six parts of pharyngeals and 49 isolated teeth from Late Pliocene of Owyhee County, Idaho: USNM 22308 and UMMP 40578. USGS loc. 20475. A complete, an almost complete, and a fragment of pharyngeals from Late Pliocene of Elmore County, Idaho: USNM 22305. USGS loc. 20195. Two parts of pharyngeals from Late Pliocene of Elmore County, Idaho; USNM 22307.

This species is known from the pharyngeals, which are very large and robust. All of the type specimens are imperfect. New collections of this species from Idaho include a perfect pharyngeal and two almost perfect ones. There is no Recent cyprinid fish in North America that has pharyngeals as large as these.

The most distinct characteristics of these bones is the mesially deflected ventral edge of the pitted surface. The relative width is about 2.5, which is very wide compared to other cyprinids in North America. The anterior limb is much shorter than the posterior limb. The tip of the anterior limb has a distinct subtriangular area for the attachment to the pharyngeal on the other side. The pitted surface extends from the space between the anterior tip and tooth IV to the space between the posterior angle and the posterior tip of the pharyngeal. The anterior and posterior angles are fairly distinct in most of the specimens. The anterior edentulous process is much shorter than the dentigerous part and almost equal to the posterior edentulous process. The posterior edentulous process makes an acute curve mesially. The dentigerous surface is much elevated posteriorly from the base of the arch. It is not clear if the minor tooth row is always present; when present, it is much reduced and rudimentary. None of the specimens has been found with the minor tooth row, though a few had the socket-like structure (alveolus) at the space between the major tooth row and the inner edge of the pitted surface. The teeth are all depressed, molariform, and covered by a smooth enamel surface. The head of the tooth is specialized for crushing and was probably employed for crushing mollusk shells. Unlike most of the cyprinids, tops of the teeth on each side oppose each other for mastication. This situation is similar to that in *Mylocheilus*. According to Dwight W. Taylor, a drastic extinction of the numerous and large molluscan fauna during Late Pliocene or Early Pleistocene readily explains the extermination of *Mylocyprinus robustus* in this region.

Following are measurements of the complete and largest specimens in the collection. USNM 22305, in mm: pharyngeal (right) length, 50.0; width, 19.4; length of dentigerous surface 30.0; length of anterior edentulous process, 21.0; length of posterior edentulous process, 22; length of longest tooth (II), 9.5; longest diameter of largest tooth (III), 10.0.

Ptychocheilus cf. *oregonensis* (Richardson)

Cyprinus (Leuciscus) oregonensis Richardson, 1836, Fauna Bor. Amer., III: 305.

Ptychocheilus oregonensis (Girard), 1856, Proc. Acad. Nat. Sci., 8: 209.

Referred materials: USGS loc. 19128. Two parts of pharyngeals and 29 isolated teeth from Late Pliocene of Owyhee County, Idaho. USNM 22287. USGS loc. 19129. Three parts of pharyngeals from Late Pliocene of Owyhee County, Idaho; USNM 22300. USGS loc. 19216. Three teeth and a part of pharyngeal from Early Pleistocene of Twin Falls County, Idaho; UMMP 40584 and UMMP 33907. USGS loc. 19217. Three teeth from Early Pleistocene of Twin Falls County, Idaho; USNM 21899. USGS loc. 21017. One part of pharyngeal from Early Pleistocene of Elmore County, Idaho; USNM 22301. USGS loc. 20475. One tooth from Late Pliocene of Elmore County, Idaho; UMMP 37189.

The identification of this species is made on the basis of the shape of the pharyngeal teeth, since none of the pharyngeals was complete. Therefore this identification is a tentative one. The tips of the teeth are posteriorly recurved and hooked. The teeth are cylindrical and neither compressed nor depressed; they have no grinding surface. There are some differences in tooth shape that depend on the position of the tooth on the bone—that is, tooth IV or V is usually conical and very slightly or not hooked, whereas tooth I is strongly hooked at the tip, which indicates that this fish is well adapted to a carnivorous food habit. Other teeth are intermediate in shape between these two types. There is a pharyngeal about four fifths complete with a narrow, pitted surface which originates from opposite tooth III. It is impossible to decide if the fossil material represents the living species *Ptychocheilus oregonensis*, but the two are very definitely closely related. The genus *Ptychocheilus* includes the largest Recent species of cyprinid fishes in North America, attaining lengths to 150 cm. The present-day distribution of *Ptychocheilus oregonensis* is the Columbia River Basin and adjacent drainages (including Malheur Lake, Oregon) northward to the Nass and Peace rivers of British Columbia. (Data furnished by Robert R. Miller.)

The length of the largest tooth in this collection is 14.3 mm. and the diameter is 3.8 mm.

Diastichus parvidens Cope

Diastichus parvidens Cope, 1870, Proc. Amer. Philos. Soc., 11: 538–547.

Referred materials: USGS loc. 19128. Four parts of pharyngeals from Late Pliocene of Owyhee County, Idaho; USNM 22302. USGS loc. 20475. One almost complete pharyngeal and two parts of pharyngeals from Late Pliocene of Idaho; USNM 22303. USGS loc. 19216. Two parts of pharyngeals from Early Pleistocene of Twin Falls County, Idaho; UMMP 40580. USGS loc. 19217. Two parts of pharyngeals from Early Pleistocene of Twin Falls County, Idaho; USNM 40581.

This species is only known by the pharyngeals. The tooth formula is 0,?–5,0 (0,4–?,?, in type description); therefore probably the complete tooth formula is 0,5–5,0 or 0,4–5,0, or 0,5–4,0.

The shape of the pharyngeal in general strongly resembles that of the subgenus *Siphateles*,[1] of the genus *Gila*. The characteristics of this bone are the

[1] The synonymizing of *Siphateles* Cope with *Gila* Baird and Girard results from my unpublished study (Osteology and Phylogeny of the American Cyprinid Fishes Allied to the Genus *Gila*) Ph.D. thesis, University of Michigan, 1960.

twisted appearance of the posterior edentulous process, with a small recurved tip which forms the distinct attachment area to the cranium. The posterior tip also has a distinct subtriangular area for the attachment to the pharyngeal on the other side. The anterior and posterior angle are more or less indistinct. The pitted surface starts from opposite tooth I and extends to the space slightly beyond the point opposite tooth V. The dentigerous part is well elevated, and the teeth are laterally compressed. Some teeth have a well-developed grinding surface. The heads of the teeth are expanded so that the distinction between head and stem is clear.

The length of the largest pharyngeal is 32.3 mm., its width 10.8 mm. The anterior edentulous process is 13.9 mm., the posterior edentulous process 16.5 mm., the anterior limb is 20.8 mm., and the posterior limb 27.8 mm.

Sigmopharyngodon, gen. nov.

Type species: *Sigmopharyngodon idahoensis*, sp. nov.

Diagnosis: A cyprinid fish with a strongly recurved tip at the posterior end of the pharyngeal—whence the generic name. All teeth have a very sharp grinding surface, even in small specimens. The tips of the teeth are not recurved or hooked but are pointed. The teeth are in one row, 0,5–5,0, and the dentigerous part is considerably elevated from the pitted surface.

Sigmopharyngodon idahoensis sp. nov.

(Fig. 2)

Holotype.—USNM 21900, a left pharyngeal with 4 teeth, (tooth I is missing). Collected by Dwight W. Taylor in 1955.

Paratypes.—USNM 22275, 7 fragments of pharyngeals and 6 isolated teeth. Same data as holotype.

Horizon and type locality.—The U. S. Geological Survey Cenozoic Locality 19213, Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. NW. ¼ Sec. 21, T. 7 S., R. 13 E. 700′ E., 100′ S. to 1150′ E., 400′ S. of NW. corner. 3097′ elev. Hagerman formation. Fossils from a 6′ bed of tan silt weathering nearly white, the lowest light-colored bed exposed in the gulch.

This species was also collected from the following localities (specimen numbers are in parentheses): USGS Cenozoic Series. 19128 (USNM 22276 & UMMP 40577), 19129 (USNM 22277), 19216 (USNM 22278), 19217 (USNM 22279), 20128 (USNM 22280), 20765 (USNM 22281), 21012 (USNM 22282), 21017 (USNM 22283), 21048 (USNM 22284), 21049 (USNM 22285), 21011 (USNM 22286).

Description of holotype.—The holotype is an almost complete, right pharyngeal lacking only the tooth I, and probably represents a small individual since larger teeth of the same species occur in other localities. The sharp-edged grinding surface on all of the teeth strongly suggests that this species was adapted to a herbivorous diet. The tooth formula seems to be 0,5–5,0. The teeth are strongly laterally compressed and the grinding surfaces are facing to dorsoposteriorly. The head and stem of the teeth are distinct, and the stem and base grade into each other.

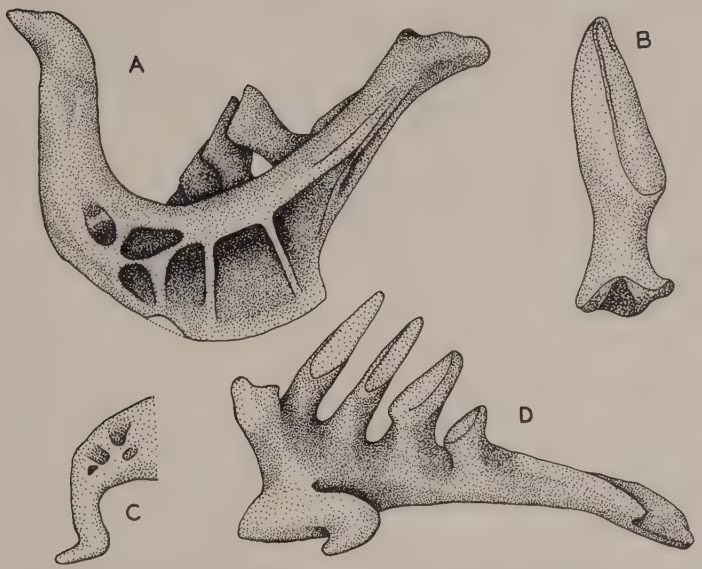

FIG. 2. *Sigmopharyngodon idahoensis* sp. nov.; *A*, holotype, USNM 21900, dorsolateral view of right pharyngeal; *B*, paratype, USNM 22275, a pharyngeal tooth; *C*, paratype, USNM 22275, dorsolateral view of posterior edentulous process showing more extreme form; *D*, dorsomesial view of holotype (*A*). *A* and *D* ×10.

The anterior angle is distinct and the posterior one is fairly distinct. The pitted surface extends anteriorly to the space between the anterior angle and the tip, and posteriorly to the posterior angle.

There are six concavities on the pitted surface. The dentigerous part is posteriorly elevated and the ventral side of each alveolus has a foramen perforated to the base of the tooth. The posterior limb is longer than the anterior limb, and the anterior and posterior edentulous processes are of the same length.

The relative width is 4.0. The major part of the head of the teeth is black.

Measurement of holotype.—Length of pharyngeal, 7.5 mm.; width of pharyngeal, 1.9 mm.; length of anterior limb, 4.5 mm.; length of posterior limb, 6.5 mm.; length of dentigerous part, 4.3 mm.; length of anterior edentulous process, 3.2 mm.; length of posterior edentulous process, 3.5 mm.; length of largest tooth (tooth II), 3.1 mm.

Description of paratypes.—The paratypes comprise the following fragments —a pharyngeal which lacks the anterior edentulous process, two pieces of the posterior edentulous processes, a pharyngeal which lacks the anterior limb and

teeth, a pharyngeal which lacks the posterior limb and teeth, a part of the dentigerous portion without teeth, a part of the anterior edentulous process, a part of the posterior limb with two teeth, and 6 isolated teeth.

Mylopharodon hagermanensis sp. nov.

(Fig. 3)

Holotype.—UMMP 40582, a left pharyngeal with teeth II, III, and IV. Collected by Claude W. Hibbard in 1956.

Paratypes.—UMMP 40583, 46 parts of pharyngeals and 10 isolated teeth. Same as holotype.

Horizon and type locality.—USGS Cenozoic Locality 20765 (DWT 540). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. SW. ¼ Sec. 28, T. 7 S., R. 13 E. 300′–400′ E., 2100′ N. of SW. corner. 3025′ elev. Fossils from higher saddle on south spur of square-nosed butte, from 2′–10′ above a conspicuous light gray platy-weathering 2″-thick carbonaceous clay shale. Clay shale is 20′ above upper pumice.

This species was also collected from the following localities: USGS Cenozoic Locality 19128 (USNM 22288, 79 parts of pharyngeals and 74 isolated teeth);

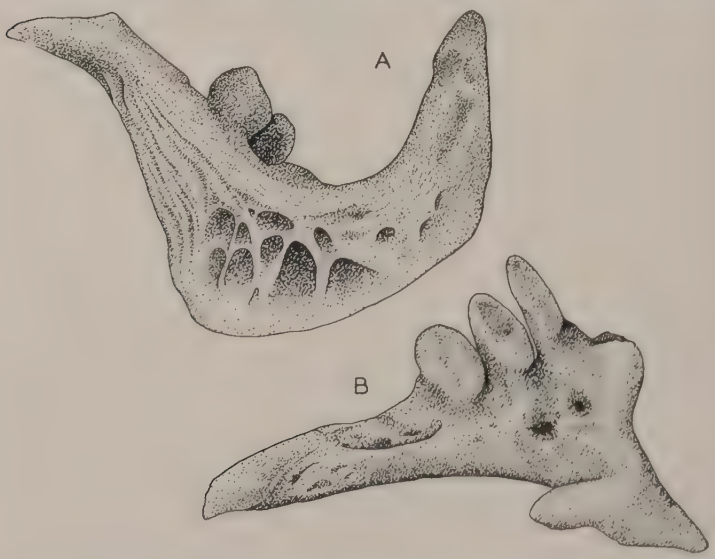

FIG. 3. Holotype of *Mylopharodon hagermanensis* sp. nov., ×5. *A*, holotype, UMMP 40582, dorsolateral view of left pharyngeal; *B*, dorsomesial view of the same.

19129 (USNM 22289, 11 parts of pharyngeals and 10 isolated teeth); 19194 (USNM 22290, 1 part of pharyngeal); 19213 (USNM 22291, 26 parts of pharyngeals and 4 isolated teeth); 19216 (USNM 22292, 13 parts of pharyngeals and 6 isolated teeth); 19217 (USNM 22293, 13 parts of pharyngeals and 12 isolated teeth); 20128 (UMMP 40579, 5 parts of pharyngeals); 20475 (USNM 22294, 1 part of pharyngeal); 20764 (USNM 22295, a part of pharyngeal); 21011 (USNM 22296, 3 parts of pharyngeals and 9 isolated teeth); 21012 (USNM 22297, a part of pharyngeal and 3 isolated teeth); 21017 (USNM 22298, a part of pharyngeal and 8 isolated teeth); 21049 (USNM 22299, a part of pharyngeal).

Diagnosis.—A species of *Mylopharodon*. The tooth formula is 2,5–4,2. The anterior edentulous process is short. The attachment area of the left and right pharyngeals is quite distinct and broad at the tip of the anterior limb. The dentigerous part is more elevated than in its living relative. The anterior and posterior angles are fairly distinct but vary from one pharyngeal to another. On posterior teeth the tips are slightly recurved and occasionally have a grinding surface. The teeth are moderately compressed and some of the anterior teeth (IV, V) have a tendency to become molariform. The size of the teeth is more uniform in this species than in *Mylopharodon conocephalus*, and the line of the minor row is more oblique against the pitted surface.

Description of holotype.—The holotype of this species is a left pharyngeal which lacks teeth I, V, (1), and (2). The anterior and posterior angles are fairly distinct. The pitted surface anteriorly extends near the tip of the anterior limb, posteriorly to the posterior angle.

Measurement of holotype.—Length of pharyngeal, 16.1 mm.; width of pharyngeal, 5.8 mm.; length of anterior limb, 11.3 mm.; length of posterior limb, 13.7 mm.; length of dentigerous part, 9.4 mm.; length of anterior edentulous process, 5.4 mm.; length of posterior edentulous process, 8.2 mm.

? *Mylopharodon* cf. *condonianus* (Cope)

Leucus condonianus Cope, 1883, Proc. Acad. Nat. Sci. Phila., pp. 134–166.

Referred material: This material came from USGS Cenozoic Locality 20095 (USNM 22304). This specimen is a right pharyngeal which lacks the posterior edentulous process, tooth I, II, V, (1) and (2). Since it is almost impossible to identify accurately this type of incomplete material, the identification is only tentative. Tooth formula is ?,?–5,2. The anterior edentulous process is rather short, much shorter than the dentigerous part. The anterior angle is not distinct. The pitted surface extends to opposite tooth V.

Teeth III and IV, still attached to the pharyngeal, are depressed and molariform. The heads of these teeth are expanded and their stems are constricted. The surface of the tooth top is smooth and flat, covered by enameloid material. The size is rather medium—the width is 11 mm., the anterior process, 10 mm., and the dentigerous part, 18 mm.

Notes on Other Cyprinid Fossils in North America

Since fossils are often very fragmentary, information obtainable from them is quite restricted when compared with data available for

Recent species. Many fossil species are based only on pharyngeals and some on specimens embedded in sedimentary rocks with only one side of the skeleton exposed. The type material of others consists of small fragments such as parts of the opercular and vertebrae. Comparable skeletal parts are not often represented among the different fossils, so that it is frequently impossible to make adequate comparisons. Furthermore, one is often uncertain whether different fragments represent more than one species.

In studying the fossil collection from Idaho, I examined many type specimens of fossil minnows from North America. I regard some of those originally placed in separate genera to be congeneric or even conspecific, and about one third of those described before 1950 appear to be referable to living genera.

The fossil species listed below are arranged in alphabetical order under their original names, followed by the authority, year reported, age, locality, and my comments. The designation "type ?" means that the particular specimen (or specimens) was not designated as the type, but the original description was evidently based on that material. The type specimens described by Cope (1870) do not now bear the Smithsonian numbers he recorded. Concerning this matter Dr. Dunkle (in a letter to Dr. Hibbard) wrote "I fail to understand the discrepancies between Cope's published numbers and our present ones, unless the latter were assigned with the establishment of several separate departments from the old all inclusive department of Comparative Zoology. You will note also that none of these have been recognized as types." Without further study I am reluctant to designate lectotypes.

The list that follows represents an attempt to summarize existing knowledge of the paleontological record of American cyprinids. It is hoped that the paucity of information presented will stimulate others to conduct research in this neglected field, in order that the zoogeography, systematics, and evolution of this large family may become better known. Species that I do not comment on are those recently described by Smith (1954, 1958) or ones I did not examine.

Specimens Mainly Based on Pharyngeals

Alburnus angustarcus Cope: Cope, 1878, Pleistocene, Fossil Lake, Oregon. Cope, 1883 (as *Cliola angustarcus*) from the same locality. AMNH 2636 (type) from American Museum of Natural History is so similar to the pharyngeals of

the subgenus *Siphateles* of the genus *Gila* that I refer it to that genus under the combination *Gila angustarca* (Cope).

Alburnops gibbarcus Cope: Cope, 1878, Pleistocene, Fossil Lake, Oregon. Cope, 1883 (as *Myloleucus gibbarcus*) from the same locality. Although I did not examine material, this species is probably a *Gila* (see under *Anchybopsis breviarcus*).

Anchybopsis altarcus Cope: Cope, 1878, Pleistocene, Silver Lake, Oregon. In AMNH 2668 (type) I did not find any significant differences from the pharyngeals of the subgenus *Siphateles*. Its name therefore becomes *Gila altarca* (Cope).

A. breviarcus Cope: Cope, 1878, Pleistocene, Silver Lake, Oregon. The form of the pharyngeals of AMNH 2667 (type) lies within the range of variation observed for the subgenus *Siphateles*. Cope himself (1883) synonymized this species with *Myloleucus gibbarcus* (= *Alburnops gibbarcus*). I therefore refer it to *Gila*.

A. latus Cope: Cope, 1870, Pleistocene, Catharine Creek, Idaho. The general features of USNM 2120 (type ?) are somewhat similar to *Diastichus parvidens*, which has a single row of teeth. It is difficult to compare the two species, however, since this specimen lacks the posterior edentulous process characteristic of *D. parvidens*.

Aphelichthys lindahlii Cope: Cope, 1893, Pleistocene ?, Pulaski County, Illinois.

Diastichus macrodon Cope: Cope, 1870, Pleistocene, Idaho. Cope, 1883, new material from the same locality. I examined USNM 2116 (type ?). This may be a good species.

D. parvidens Cope: Cope, 1883, Pleistocene, Idaho. Uyeno (in this report). I examined USNM 2114 (type ?). This is a good, distinguishable species characterized by the somewhat twisted appearance of the posterior edentulous process.

D. strangulatus Cope: Cope, 1883, Pleistocene, southern Idaho. In AMNH 2764 (type) only parts of pharyngeals are represented, and it is very difficult to determine the status of this species.

? *Hybopsis* cf. *gracilis* (Richardson): Smith, 1958, Pleistocene, Harper County, Oklahoma.

Leucus condonianus Cope: Cope, 1883, Pleistocene, Oregon. I examined AMNH 2756 (type). The general form is somewhat similar to the genus *Mylopharodon*, but the specimen is so incomplete that it cannot be compared with other specimens in detail.

Mylocyprinus inflexus Cope: Cope, 1883, Pleistocene, near Sinker Creek, Idaho. An examination of AMNH 2741 (type) revealed great differences between these pharyngeals and those of *Mylocyprinus robustus* Leidy. I do not feel that this species is congeneric with *M. robustus*; further studies are necessary to place it generically.

M. kingii Cope: Cope, 1870, Pleistocene, Catharine Creek, Idaho. I examined USNM 2118 (type ?) and recognized that this is identical with *M. robustus*; it is therefore synonymized with that species. The relative size of tooth I (fourth

tooth of Cope), used as the sole distinguishing character, is too variable to be of specific value.

M. longidens Cope: Cope, 1870, Pleistocene, Catharine Creek, Idaho. I did not examine the type specimens, but judging from the original description, I think that this is also a synonym of *M. robustus*.

M. robustus Leidy: Leidy, 1870, Pleistocene, Idaho. I examined AMNH 7529. Though the size is extraordinarily large, the general morphological features of the pharyngeal is quite close to the Recent genus *Mylocheilus*.

? *Mylopharodon condonianus* (Cope): Uyeno (in this report; this species is equal to *Leucus condonianus* Cope), Pleistocene, Owyhee County, Idaho.

M. hagermanensis sp. nov.: Uyeno (in this report), Early Pleistocene, Twin Falls County, Idaho.

Notemigonus crysoleucas (Mitchill): Smith, 1954, Pleistocene, Beaver County, Oklahoma.

Oligobelus arciferus Cope: Cope, 1870, Pleistocene, Idaho. I examined only USNM 2115, which is identical with *Mylocyprinus robustus*, but this is probably not the type specimen since it does not seem to agree with the original description.

O. laminatus Cope: Cope, Pleistocene, Idaho. Cope, 1883, Pleistocene, Idaho Lake, Idaho (as *Squalius laminatus*). USNM 2122 (type ?) is too fragmentary for a confident identification. Therefore it would be desirable to examine the more complete material reported by Cope, 1883.

Pimephales promelas Rafinesque: Smith, 1958, Pleistocene, Harper County, Oklahoma.

Ptychocheilus cf. *oregonensis* (Richardson): Uyeno (in this report). Late Pliocene and Early Pleistocene, Idaho.

Semotilus sp.: Smith, 1954, Pleistocene, Beaver County, Oklahoma.

S. bairdii Cope: Cope, 1870, Pleistocene, Idaho. Cope, 1883 (as *Squalius bairdi*), Pleistocene, Idaho.

S. posticus Cope: Cope, 1870, Pleistocene, Idaho. Cope, 1883 (*Squalius posticus*), Pleistocene, Idaho. I identify USNM 2113 (type ?) as *Ptychocheilus* sp.

Sigmopharyngodon hagermanensis sp. nov.: Uyeno (in this report). Early Pleistocene, Twin Falls County, Idaho.

Squalius reddingi Cope: Cope, 1883, Pleistocene, southern Idaho. I identify AMNH 2767 (type) as *Ptychocheilus* cf. *oregonensis*.

Species Based on Fossils Embedded in Sedimentary Rocks

Leuciscus rosei Hussakof: Hussakof, 1916, Miocene, British Columbia.

L. turneri Lucas: Lucas, 1900, Pliocene, Nevada.

Ptychocheilus tularis Jordan: 1927, Jordan, Pleistocene ?, California.

Recorded by Name Only

Mylopharodon conocephalus (Baird & Girard): Sinclair, 1904, Pleistocene, Potter Cave, California.

Ptychocheilus (?) *grandis* (?) (Ayers): Sinclair, Pleistocene, Potter Cave, California.

Siphateles mohavensis Snyder: Blackwelder & Ellsworth, 1936, Pleistocene, Manix Lake, California.

MISCELLANEOUS

Anchybopsis fasciolatus Cope: Russell, *nomen nudum* (Hay, 1929).

Alisodon mirus Hay: Hay, 1920, not a fish bone.

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LITERATURE CITED

BLACKWELDER, ELIOT, AND ELMER W. ELLSWORTH. 1936. Pleistocene Lakes of the Afton Basin, California. Amer. Jour. Sci., 31: 453–463, figs. 1–4.

CHU, YUANTING T. 1935. Comparative Studies on the Scales and on the Pharyngeals and Their Teeth in Chinese Cyprinids, with Particular Reference to Taxonomy and Evolution. Biol. Bull. St. John's Univ. No. 2: 1–225, figs. 1–244.

COPE, EDWARD D. 1870. On the Fishes of a Freshwater Tertiary in Idaho, Discovered by Capt. Clarence King. Proc. Amer. Philos. Soc., 11: 538–547.

——. 1878. Description of New Vertebrata from the Upper Tertiary Formations of the West. *Ibid.*, 17: 219–231.

——. 1883. On the Fishes of the Recent and Pliocene Lakes of the Western Part of the Great Basin, and of the Idaho Pliocene Lake. Proc. Acad. Nat. Sci. Phila., 1883: 134–166.

——. 1893. A New Extinct Species of Cyprinidae. *Ibid.*, 1893: 19–20.

Dorf, Erling. 1959. Climatic Change of the Past and Present. Contr. Mus. Paleo. Univ. Mich., 13(8): 181–210, figs. 1–3, maps 1–7, Pl. 1.

Hay, Oliver P. 1920. Descriptions of Some Pleistocene Vertebrates Found in the United States. Proc. U.S. Nat. Mus., 58: 83–146, pls. 3–11, figs. 1–4.

——. 1929. Second Bibliography and Catalogue of the Fossil Vertebrata of North America. Vol. I. Carnegie Inst. Wash., 1–916.

Hibbard, Claude W. 1959. Late Cenozoic Microtine Rodents from Wyoming and Idaho. PMASAL, 44 (1958): 3–40, figs. 1–7.

Hussakof, L. 1916. A New Cyprinid Fish, *Leuciscus rosei*, from the Miocene of British Columbia. Amer. Jour. Sci., (4) 42: 18–20, fig. 1.

Jordan, David S. 1907. The Fossil Fishes of California; with Supplementary Notes on Other Species of Extinct Fishes. Bull. Dept. Geol., Univ. Calif., 5: 95–145, figs. 1–33, pls. 11–12.

——. 1927. The Fossil Fishes of the Miocene of Southern California. Contribution 9, Stanf. Univ. Publ. Univ. Ser. Biol. Sci., 5(2): 85–99, pls. 1–4.

Leidy, Joseph. 1870. (Remarks on Fossil Vertebrates). Proc. Acad. Nat. Sci. Phila., 1870: 69–71.

Lucas, Frederic A. 1900. A New Fossil Cyprinid, *Leuciscus turneri*, from the Miocene of Nevada. Proc. U.S. Nat. Mus., 23: 333–334, pl. 8.

Miller, Robert Rush. 1959. Origin and Affinities of the Freshwater Fish Fauna of Western North America. Zoogeography, Amer. Assoc. Adv. Sci., Publ. 51: 187–222, figs. 1–19.

Russel, Israel C. 1902. Geology and Water Resources of the Snake River Plains of Idaho. Bull. U.S. Geol. Surv., No. 199: 1–192, figs. 1–6, pls. 1–25.

Sinclair, William J. 1904. The Exploration of the Potter Cave. Univ. Calif. Publ. Amer. Archaeol. and Ethnol., 2(1): 1–27, pls. 1–14.

Smith, C. Lavett. 1954. Pleistocene Fishes of the Berends Fauna of Beaver County, Oklahoma. Copeia, 1954(4): 282–289, figs. 1–7.

——. 1958. Additional Pleistocene Fishes from Kansas and Oklahoma. *Ibid.*, 1958(3): 176–180, figs. 1–3.

Stearns, H. T. 1936. Origin of the Large Springs and Their Alcoves Along the Snake River in Southern Idaho. Jour. Geol., 44(4): 429–450, figs. 1–8.

Wilson, Robert W. 1933. A Rodent Fauna from Later Cenozoic Beds of Southwestern Idaho. Carnegie Inst. Wash. Pub., No. 440: 117–135, pls. 1–2, figs. 1–8.

Yen, T. C. 1944. Notes on Fresh-water Mollusks of Idaho Formation at Hammett, Idaho. Jour. Paleont., 18: 101–108, figs. 1–12.

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EVOLUTION OF THE DORSAL-FIN SUPPORTS OF PERCOID FISHES*

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Many teleost fishes have one or more awl-shaped bony elements lying in the sagittal plane anterior to the dorsal fin. These have been termed the predorsal interneural bones, but Eaton (1945) has suggested that interneural and interhemal as applied to fin supports have no particular morphological value, and we may add that they are not always entirely appropriate. The term predorsal bones seems adequate. The number and form of the predorsal bones vary, but they are usually slender and elongate with the long axis more or less vertical. In some species the predorsals resemble the pterygiophores of the dorsal fin, but in others they are merely small rods. In some forms they are T-shaped; in others they are specialized, shaped like an inverted letter L with the short arm directed forward and pointed at its tip. In a few genera the homologous projection of the first pterygiophore is much enlarged and may be exposed (e.g., *Scatophagus*, *Hapalogenys*). This structure is commonly termed a procumbent spine and has been included as part of the dorsal-fin formula by some authors.

The nature and origin of the predorsal bones have been discussed by several authors (e.g., Bridge, 1896; Eaton, 1945; Lindsey, 1955), and it is generally conceded that in most teleosts these elements are rayless pterygiophores. The problem is complicated by the fact that in lower fishes, e.g., *Leptolepis dubius* (Goodrich, 1930, fig. 90) and *Palaeoniscus macropomus* (Eaton, 1945, fig. 4), there may be two series of median bones between the neural arches and the dorsal fin—the supraneurals and the pterygiophores. The supraneurals commence on the first vertebra, are juxtaposed to the neural arches, and usually correspond in number and arrangement to these arches as far as they extend. In *Lepisosteus* the supraneurals are associated with predorsal vertebrae, sometimes as far back as those below the

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anterior dorsal pterygiophores, where the bones of the two series may interdigitate but remain distinct. In *Amia calva* the strict numerical correspondence of the supraneurals and neural arches is lost after about the fifth vertebra, but the serial homology with the remaining elements, about 5 in number, seems clear. In this species the posterior supraneural lies several vertebrae in front of the anterior dorsal pterygiophore, the bones of the two series being well differentiated. Therefore, we agree with Eaton (1945, p. 205) in interpreting the bones of the anterior series in *Amia* as supraneurals rather than as radials (pterygiophores), as contended by Goodrich (1930, p. 89). Most teleosts lack serial correspondence of vertebrae and proximal pterygiophores (Eaton, 1945, p. 207; Lindsey, 1955, pp. 40–41). In the osteoglossid, *Arapaima gigas*, however, the dorsal fin is situated well back on the body and the series of pterygiophores extends forward as predorsal bones, one opposed to and articulated with each neural spine except for those of the first two vertebrae. Since the ray-bearing and predorsal bones are apparently in serial homology, the latter may be regarded as vestigial supports of a previously elongate fin rather than as supraneurals. It may be concluded that the predorsal bones of teleosts are homologous with the proximal pterygiophores of the dorsal fin.

In order to assess the possible usefulness of the predorsal bones as taxonomic characters within the superfamily Percoidea, the condition of these bones has been studied in 223 species representing 47 families of these spiny-rayed fishes. These data reveal definite trends within this group and contribute to an understanding of the nature of these bones.

Methods and Materials

Most of the data presented here are taken from X-ray skiographs (shadow images) although some were obtained from specimens cleared in potassium hydroxide and stained with alizarin. The use of X-ray photography has permitted the rapid examination of large numbers of individuals without destructive and time-consuming dissections. Dried skeletal preparations are of dubious reliability because of possible loss of predorsal bones, which have neither articular nor strong ligamentous connections with neighboring bones. Numerical data on predorsal bones and pterygiophores are recorded as simple formulae, each numeral indicating the numbers of fin rays supported by that

predorsal or pterygiophore. For example, the formula for a specimen in which there are 3 predorsals, 2 spines on the first proximal pterygiophore and a single spine on each of the succeeding proximal pterygiophores is: 0–0–0–2–. The terminal dash indicates that each remaining pterygiophore supports one ray.

The Dorsal-fin Supports and the Fin Rays

Primitively, in spiny-rayed fishes, three series of bony elements contribute to the support of the dorsal fin (Pl. 1*A*). The proximal series consists of elongate bones which approximate the tips of the neural spines or interdigitate with them, at least at the anterior end of the fin. These are the proximal pterygiophores or basals. The second series, the intermediate pterygiophores, are shorter bones that are fused with the basals in most adult percoids but are discrete in the young and remain separate posteriorly in some species. The distal series consists of short bones or blocks of cartilage lying between the bases of the right and left components of the dorsal rays. In higher teleosts, there is general serial correspondence between pterygiophores and dorsal- and anal-fin rays although the relationship is frequently altered at one or both ends of the fin.

The dermal elements supporting the membrane of the fin itself are properly called lepidotrichs and are of two general types, spines and soft rays. There is little fundamental difference between them, and intermediate conditions exist. Ontogenetic transition between the two types has been demonstrated in *Roccus saxatilis* and reported in other species (Mansueti, 1958). Soft rays are articulated (consisting of short segments), are usually branched, and have discrete right and left halves. Spines are nonsegmented, are unbranched, and have the right and left sides consolidated although the line of fusion is often represented by a groove.

There is progressive modification of the dorsal fin anteriorly. Posteriorly the pterygiophores are slender, and elements of the three series tend to be distinct (the ultimate support is an exception). Anteriorly the proximal and intermediate pterygiophores are completely fused and are expanded into broad plates, usually with one or more stiffening keels on each side. Posteriorly the distal pterygiophores are mere blocks of cartilage. Anteriorly they are intricately formed bones, each with a peglike posterior projection that penetrates the base of the spine. The posterior lepidotrichs or soft rays are ca-

pable of lateral inclination, but the spinous anterior rays have restricted lateral movement, although they can be erected and depressed. Thus, the posterior part of the fin may serve in propulsion; the anterior part forms a more or less rigid, stabilizing keel. In many percoid fishes the stiffening of the leading edge of the fin is increased by having the first two spines supported by a single pterygiophore, thus minimizing motion between these spines.

Although there is a one-to-one correspondence between the fin rays and their supports (Lindsey, 1955), the rays have shifted posteriorly so that their support is compound, i.e., the bases of the fin rays alternate with the distal ends of the pterygiophores. In most percoids the rays are more closely associated with the pterygiophore of the next posterior ray than with their own, but the fundamental association is clear from the alignment of elements of the three series of pterygiophores (Pl. I*B*). As a result of this backward shift, the proximal segment of the first pterygiophore no longer supports a fin ray. Subsequent loss or fusion of the distal and middle segments leaves this basal as a predorsal bone.

Thus, at least one predorsal bone is a pterygiophore that has lost its lepidotrich through a backward shift of the rays. If this is the only source of the predorsal bones, and there is nothing in their appearance or arrangement to suggest otherwise, it would appear that the primitive number of predorsal bones is one. This may be true for spiny-rayed fishes in general, but in the superfamily Percoidea the only forms with this arrangement also have modifications of the body or fins that suggest that the condition is secondary.

Basic Patterns of Anterior Fin Supports

Two arrangements occur with such frequency and in species that are so generalized (i.e., without obvious specializations of the dorsal fin region) as to suggest that they are the basic patterns for the superfamily Percoidea. These formulae are 0–0–1–1–1–, occurring in 5 families, and 0–0–0–2–1–, occurring in 28 of the 47 families examined. In both arrangements the first five elements support a total of 3 fin spines. The 0–0–0–2– arrangement is presumably derived from the 0–0–1– plan by a backward shift of the first spine, probably as a selective response to a need for additional stiffening of the leading edge of the fin (Pl. I*C* and *H*). An alternative explanation, that the presence of 2 spines on the first pterygiophore results from fusion of

supporting elements, is not substantiated by the positional relationship between the neural spines and anterior pterygiophores. Moreover, if fusion had occurred one would not expect the observed increase in number of predorsals. The possibility that the first spine is a *de novo* structure, developed without supporting pterygiophores, is inconsistent with the general stability of perciform fins.

Specialized Patterns of Anterior Fin Supports

From these two basic plans, the primitive 0–0–1– and the derived 0–0–0–2–, specialization has proceeded in different directions. In one trend there has been a shortening of the dorsal fin through loss of anterior spines. This results in an increase in the number of predorsals, well illustrated by the centrarchid genus *Pomoxis*. Species of this genus usually have 6 to 8 dorsal spines and 6 or 7 predorsal bones. These species are extreme but others have patterns of 0–0–0–1–(e.g., *Pomatomus*), 0–0–0–0–1–(*Toxotes*), 0–0–0–0–0–1–(*Oligoplites*), and 0–0–0–0–0–0–1–(*Vomer*). In *Pomoxis*, *Oligoplites*, and *Vomer* the reduction in length of the spinous part of the dorsal fin is obvious; in others it may be less marked.

In another direction of change there has been reduction in the number of predorsal bones. Simple loss of the predorsals is well illustrated by the Percidae. The Eocene genus *Mioplosus*, although more or less intermediate between the Centrarchidae and the Percidae, seems properly allocated to the latter family. A specimen of *Mioplosus* sp. from Fossil, Wyoming (University of Michigan, Museum of Paleontology, No. 8405) has the anterior dorsal formula 0–0–1–, the postulated basic arrangement among percoids. In the larger Recent members of the family (*Stizostedion*, *Perca*, and *Acerina*) there is usually only one predorsal bone (0–1–), and the highly specialized darters, *Ammocrypta*, *Etheostoma*, and *Percina*, have lost all predorsal elements (1–); Pl. I*C*, *D*, and *E*). The specialized dwarf centrarchids of the genus *Elassoma* also have lost all or all but one of the predorsals. Loss of predorsals is frequently associated with the attainment of a terete body shape, as in the percids, *Elassoma*, and *Rachycentron*, but parallel loss has occurred sometimes in highly compressed fishes in which the supraoccipital crest is extended backward, for example in the Leiognathidae. Reduction in the number of predorsals may have evolved also from the 0–0–0–2– arrangement (Pl. I*H*, *I*, and *J*).

A reduced number of predorsal bones may result also from ante-

rior extension of the dorsal fin, as in the dolphin, *Coryphaena* (Pl. 1*K*). This specialization could conceivably be achieved through repossession of predorsals by new dorsal spines. It seems more plausible, however, that new spines and their supporting pterygiophores have been added to the series, and that predorsal bones previously present have been forced out.

Thus, both predorsal bones and dorsal spines may be lost independently and perhaps jointly, combination units (spines and supporting pterygiophores) may be added to the system, and spines may be shifted backward so that two or even three are borne by a single pterygiophore. In view of these rather fluid relations it is probably impossible to discern the precise evolutionary history of many phyletic lines.

Intraspecific Variation

In a few species there may be variation in the numbers of predorsal elements or in the number of spines supported by the first ray-bearing pterygiophore. In general there is more intraspecific variation in those species with modified plans than among those with the basic arrangements (0–0–1– and 0–0–0–2–). A backward shift in position of the anterior dorsal spine may increase by one the number of predorsal bones and in consequence increase the number of spines borne by the first pterygiophore. This shift occurs as an individual variation within species (e.g., *Lepomis humilis*) as well as between related species. Loss or addition of a dorsal spine, a common individual variation in some species, may change by one the number of predorsals (e.g., *Cichlasoma salvini*, *Pomoxis annularis*). Alternatively, it may modify only the number of spines on the first pterygiophore. For example, in a series of *Pomoxis nigromaculatus*, 12 specimens have 7 dorsal spines. Of these 10 have the formula 0–0–0–0–0–0–1–, 1 has 0–0–0–0–0–0–2–, and 1 has 0–0–0–0–0–0–0–1–. Twelve other specimens have 8 dorsal spines. Of them 3 have 0–0–0–0–0–0–1– and 9 have 0–0–0–0–0–0–2–.

Evolution of Fin Supports in the Centrarchidae

The centrarchid fishes display substantial variations in number and arrangement of predorsal bones and dorsal spines. Trends in the evolution of these structures may be assessed conveniently because the phyletic relations of the group are rather well understood (Bailey, MS.). Among the 10 Recent genera of the Centrarchidae, 6 regularly

or frequently display the arrangement 0–0–0–1–, and 2 others have 0–0–0–2 -, a modification achieved by the addition of a second spine to the first dorsal pterygiophore (Fig. 1). The species of these genera have modal counts of from 9 to 12 dorsal spines. On the basis of these data and the trends in other characters we believe that the basic stock in the Centrarchidae had the pattern 0–0–0–1– and 10 dorsal spines.

All genera of the subfamily Lepominae (*Chaenobryttus, Lepomis,*

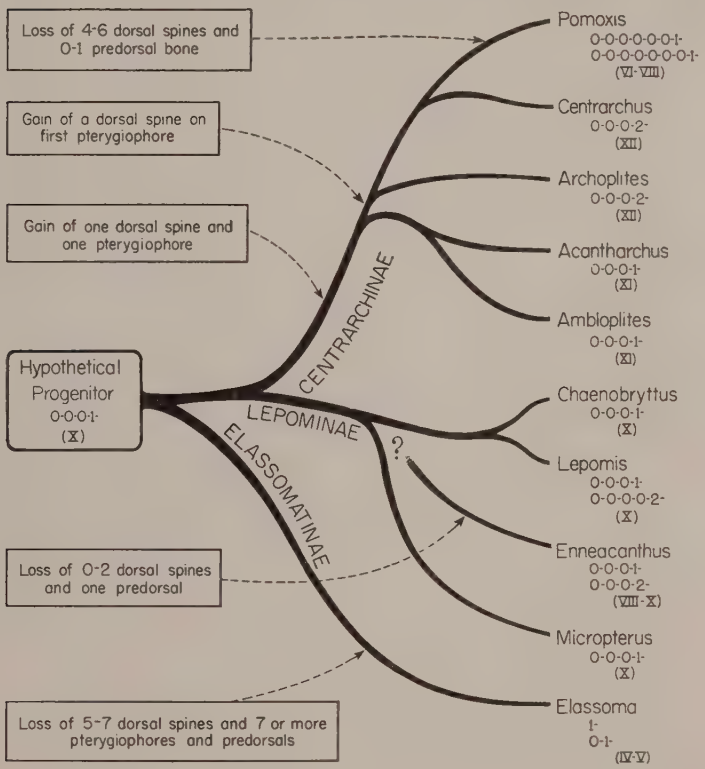
Loss of 4-6 dorsal spines and 0-1 predorsal bone
Gain of a dorsal spine on first pterygiophore
Gain of one dorsal spine and one pterygiophore
Hypothetical Progenitor 0-0-0-1- (X)
CENTRARCHINAE
LEPOMINAE
ELASSOMATINAE
?
Loss of 0-2 dorsal spines and one predorsal
Loss of 5-7 dorsal spines and 7 or more pterygiophores and predorsals
Pomoxis 0-0-0-0-0-0-1- 0-0-0-0-0-0-0-1- (VI-VIII)
Centrarchus 0-0-0-2- (XII)
Archoplites 0-0-0-2- (XII)
Acantharchus 0-0-0-1- (XI)
Ambloplites 0-0-0-1- (XI)
Chaenobryttus 0-0-0-1- (X)
Lepomis 0-0-0-1- 0-0-0-0-2- (X)
Enneacanthus 0-0-0-1- 0-0-0-2- (VIII-X)
Micropterus 0-0-0-1- (X)
Elassoma 1- 0-1- (IV-V)

FIG. 1. Evolution of anterior dorsal elements in the Recent genera of the family Centrarchidae. For each genus there are indicated the formula(e) of predorsal bones and fin supports and, in parentheses, the usual or modal numbers of dorsal spines.

Enneacanthus, *Micropterus*) have the pattern 0–0 0–1– and 10 dorsal spines. The latter vary occasionally to 9 or 11 in many of the included species, and in *Enneacanthus* 8 or 9 are characteristic dorsal-spine counts. Observed variations in pterygiophore pattern include 0–0–0–0–2– in 2 among 5 specimens of *Lepomis humilis*, a backward shift of the anterior spine. In *Enneacanthus* the formulae 0–0–0–1– and 0–0–0–2– are common. The former is always associated with a reduced number of dorsal spines, 8 or 9. It is apparent that one predorsal bone has been lost in this genus. Differentiation in the subfamily involves chiefly characters other than fins. The anal fin is relatively constant in length, position, and especially in the typical complement of 3 spines.

The subfamily Elassomatinae includes only *Elassoma*, pygmy sunfishes that have notable structural modification in many size-related characters. As in the Lepominae there are 3 anal spines, but the dorsal spines have been reduced to only 3 to 5 and the predorsal bones are absent or are reduced to 1 (1– or 0–1–). Five or more dorsal spines and 7 or more pterygiophores have been lost from the primitive complement.

The remaining 5 genera constitute the Centrarchinae, characterized chiefly by the increase from a primitive 3 anal spines to from 5 to 9. Study of skiographs indicates that the additional spines have been added, together with their supporting pterygiophores, at the anterior end of the anal fin, which originates well forward on the ventral surface. We infer, in part by analogy, that the longer spinous dorsal fins of 4 of the genera result from the parallel addition of dorsal spines and supporting pterygiophores. One spine and its pterygiophore were probably added early to the main line of the subfamily, giving the 11 dorsal spines and 0–0–0 1– arrangement of *Ambloplites* and *Acantharchus*. Subsequent addition of a spine to the first functional pterygiophore of the remaining line provided the 12 dorsal spines and the formula 0–0–0 2– that are characteristic of *Archoplites* and *Centrarchus*. In *Pomoxis* the dorsal fin has only 5 to 9, usually 6 to 8 spines, and there are 6 or 7 large, T-shaped predorsal bones (formulae 0–0–0–0–0–0–1– or 0–0–0–0–0–0–0–1–). The upper arms of these bones coincide closely with the predorsal contour.

In the Centrarchidae study of anterior dorsal elements and supporting structures reveals trends that are consistent with interpretations

based on other characters, and serves to reinforce phyletic conclusions previously drawn.

Summary and Conclusions

A study of the predorsal bones and the anterior dorsal pterygiophores of 223 species of percoid fishes representing 47 families reveals certain trends in the number and arrangement of these elements. The formulae 0–0–1– and 0–0–0–2– appear more frequently than others and are considered basic patterns of the superfamily Percoidea. The formula 0–0–1– is probably primitive and from it the arrangement 0–0–0–2– has been derived by a simple backward shift of the first spine, a change conferring selective advantage since it results in increased rigidity of the leading edge of the dorsal fin. This furnishes support to the general hypothesis that the predorsal bones are rayless pterygiophores rather than disjunct supraneural bones because the additional predorsal of the 0–0–0–2–1– plan is indistinguishable from the two of the 0–0–1–1–1– pattern.

Primary trends in the Percoidea include the loss of spines with consequent increase in number of predorsals, the loss of predorsals from the 0–0–0–2–1– pattern, and loss of predorsals from the 0–0 1–1–1– scheme. Anterior extension of the dorsal fin, itself a secondary trend, may result in a reduction of predorsal elements. Often these trends are correlated with some obvious modification of body form or dorsal-fin configuration. Intraspecific variations in pterygiophore pattern are more frequent in those forms that have a modified formula than among those with a basic plan.

The relative numbers of pterygiophores, predorsals, and vertebral spines are influenced by the total numbers of these elements so that their significance is obscure at this general (superfamily) level. The evolution of anterior dorsal elements in the family Centrarchidae is consistent with relationships determined through use of other characters.

LITERATURE CITED

Bridge, T. W. 1896. The Mesial Fins of Ganoids and Teleosts. Jour. Linn. Soc. London, Zool. 25: 530–602, pls. 21–23.

Eaton, Theodore H. 1945. Skeletal Supports of the Median Fins of Fishes. Jour. Morph., 76(3): 193–212, 5 figs.

Goodrich, Edwin S. 1930. Studies on the Structure and Development of Vertebrates. London: Macmillan and Co. xxx + 837 pp.

Lindsey, C. C. 1955. Evolution of Meristic Relations in the Dorsal and Anal Fins of Teleost Fishes. Trans. Royal Soc. Canada, 49 (Ser. 3): 35–49, 2 figs.

Mansueti, Romeo. 1958. The Development of Anal Spines and Soft-Rays in the Young Striped Bass, *Roccus saxatilis*. Chesapeake Biol. Lab., Contr. 113: 1–12, 4 figs.

APPENDIX I

Relationships of Dorsal-fin Spines, Predorsal Bones, and Dorsal Pterygiophores in the Families of the Superfamily Percoidea.

Families are listed in alphabetical sequence both for convenience and because the interrelationships and phylogeny of the group are poorly understood. Several additional families are omitted because no specimens were available. For each family there are listed the formulae of anterior dorsal elements observed in the material studied and, in parentheses, the number of species in which any particular arrangement was observed. Species investigated are listed in Appendix II. In the formulae each antecedent zero indicates one predorsal bone, the numeral indicates the number of spines borne by the first pterygiophore; thereafter each pterygiophore bears one dorsal spine.

Acropomatidae: 0–0–0–2– (1)
Apogonidae: 0–0–1– (1)
0–0–0–2– (1)
Banjosidae: 0–0–2– (1)
Bramidae: 0–0–0–0–1– (1)
Branchiostegidae: 0–0–2– (2)
Carangidae: 0–0–0–1– (4)
0–0–0–2– (10)
0–0–0–0–1– (1)
0–0–0–0–0–1– (1)
0–0–0–0–0–0–1– (1)
Centrarchidae: 1– (2)
0–1– (1)
0–0–0–1– (10)
0–0–0–2– (5)
0–0–0–3– (1)
0–0–0–0–2– (1)
0–0–0–0–0–0–1– (2)
0–0–0–0–0–0–2– (1)
0–0–0–0–0–0–0–1– (2)
Centropomidae: 0–0–1– (2)
0–0–0–2– (1)

Chaetodontidae: 0–2– (1)
0–3– (1)
0–0–2– (1)
0–0–0–2– (1)
Cichlidae: 0–1– (2)
0–0–1– (13)
0–0–0–1– (2)
Coryphaenidae: 1– (1)
Drepanidae: 0–0–0–2– (1)
Emmelichthyidae: 0–0–1– (1)
0–0–0–2– (1)
Ephippidae: 0–0–0–2– (1)
0–0–0–3– (1)
Gerridae: 0–0–0–2– (11)
Girellidae: 0–0–0–2– (1)
Histiopteridae: 0–0–2– (1)
Kuhliidae: 0–0–0–2– (2)
Kyphosidae: 0–0–0–2– (1)
Labracoglossidae: 0–0–0–2– (1)
Leiognathidae: 0–1– (7)
Lethrinidae: 0–0–2– (1)
0–0–0–2– (1)
Lobotidae: 0–0–0–2– (2)
Lutjanidae: 0–0–0–2– (1)
Menidae: 0–0–0–1– (1)
Monodactylidae: 0–0–0–1– (1)
Mullidae: 0–0–0–2– (1)
Nandidae: 0–0–0–2– (2)
Nemipteridae: 0–0–2– (3)
0–0–0–2– (1)
Oplegnathidae: 0–0–0–2– (2)
Pempheridae: 0–0–0–1– (1)
Percichthyidae: 0–0–0–1– (1)
Percidae: 1– (14)
0–1– (6)
Platacidae: 0–0–0–2– (1)
Plesiopidae: 0–0–2– (2)
Pomadasyidae: 0–0–0–2– (9)
Pomatomidae: 0–0–0–1– (1)
0–0–0–2– (1)
Priacanthidae: 2– (2)
Rachycentridae: 1– (1)
Scatophagidae: 0–0–2– (1)
Sciaenidae: 0–0–0–2– (4)
Scorpidae: 0–0–0–2– (2)
Serranidae: 0–1– (1)
0–0–1– (31)

0–0–2– (3)
0–0–0–1– (4)
0–0–0–2– (20)
Sillaginidae: 0–0–0–1– (1)
Sparidae: 0–0–0–2– (2)
Theraponidae: 0–0–0–1– (1)
0–0–0–2– (2)
Toxotidae: 0–0–0–0–1– (1)

APPENDIX II

Arrangement of Dorsal-fin Spines, Predorsal Bones, and Dorsal Pterygiophores in Certain Percoid Fishes.

Species with a common formula are grouped. The sequence is alphabetical to families, genera, and species. Species displaying individual variation in formula are listed under each such variant arrangement. Museum locations of the specimens or lots studied are given. Most specimens are in the Museum of Zoology of the University of Michigan (UMMZ); others are in the Academy of Natural Sciences of Philadelphia (ANSP), the Museum of Comparative Zoology (MCZ), and the United States National Museum (USNM). For an explanation of formulae see Appendix I.

Formula 1–:

Centrarchidae: *Elassoma evergladei* Jordan, UMMZ 87886
E. zonatum Jordan, UMMZ 161086
Coryphaenidae: *Coryphaena hippurus* Linnaeus, UMMZ 176782
Percidae: *Ammocrypta beani* Jordan, UMMZ 155344
A. clara Jordan and Meek, UMMZ 76089
A. pellucida (Putnam), UMMZ 66562
A. vivax Hay, UMMZ 157816
Etheostoma acuticeps Bailey, UMMZ 159013–14
E. atripinne (Jordan), UMMZ 96351
E. blennioides Rafinesque, UMMZ 85545
E. camurum (Cope), UMMZ 160642
E. cinereum Storer, UMMZ 121708
E. maculatum Kirtland, UMMZ 159011
E. nigrum Rafinesque, UMMZ 158978
Percina aurantiaca (Cope), UMMZ 156985
P. caprodes (Rafinesque), UMMZ 158976
P. notogramma (Raney & Hubbs), UMMZ 144697
Rachycentridae: *Rachycentron canadum* (Linnaeus), UMMZ 176766

Formula 2–:

Priacanthidae: *Priacanthus cruentatus* (Lacépède), UMMZ 172731
P. hamrur (Forskål), UMMZ 176752

Formula 0–1–:

Centrarchidae: *Elassoma zonatum* Jordan, UMMZ 161086
Cichlidae: *Cichlasoma hyorhynchum* Hubbs, UMMZ 143900
C. meeki (Brind), UMMZ 102110
Leiognathidae: *Gazza minuta* (Bloch), UMMZ 176764
Leiognathus brevirostris (Valenciennes), UMMZ 176761
L. elongatus Smith & Pope, UMMZ 176797
L. equulus (Forskål), UMMZ 176773
L. leuciscus (Günther), UMMZ 176763
L. nuchalis (Temminck & Schlegel), UMMZ 142725
L. ruconius (Hamilton-Buchanan), UMMZ 176765
Percidae: *Acerina cernua* (Linnaeus), UMMZ 174629
Perca flavescens (Mitchill), UMMZ 82587
P. fluviatilis Linnaeus, UMMZ 159289
Stizostedion canadense (Smith), UMMZ 139955
S. lucioperca (Linnaeus), UMMZ 169003
S. vitreum glaucum Hubbs, UMMZ 157232
S. vitreum vitreum (Mitchill), UMMZ 171121-S

Formula 0–2–:

Chaetodontidae: *Holacanthus ciliaris* (Linnaeus), UMMZ 174165

Formula 0–3–:

Chaetodontidae: *Holacanthus chapmani* Herre, UMMZ 100225

Formula 0–0–1–:

Apogonidae: *Cheilodipterus affinis* Poey, UMMZ 174082
Centropomidae: *Chanda interrupta* (Bleeker), UMMZ 171822
Lates calcarifer (Bloch), UMMZ 171818
Cichlidae: *Cichlasoma affine* (Günther), UMMZ M59-29
C. aureum (Günther), UMMZ M59-43
C. callolepis (Regan), UMMZ M59-43
C. champotonis Hubbs, UMMZ 102203
C. cyanoguttatum (Baird & Girard), UMMZ 169614
C. ellioti Meek, UMMZ 162471
C. guttulatum (Günther), UMMZ M59-29
C. helleri (Steindachner), UMMZ M59-34
C. hyorhynchum Hubbs, UMMZ 95519
C. nebuliferum (Günther), UMMZ M59-29
C. salvini (Günther), UMMZ M59-43
Petenia splendida Günther, UMMZ 144110
Pterophyllum eimecki Ahl, UMMZ 162860

Emmelichthyidae: *Emmelichthyops atlantica* Schultz, UMMZ 174143
Serranidae: *Alphestes afer* (Bloch), UMMZ 167115
Cephalopholis fulva (Linnaeus), UMMZ 172738
Cromileptes altivelis (Valenciennes), UMMZ 100433
Dermatolepis inermis (Valenciennes), UMMZ 172574
Diploprion bifasciatus Kuhl & Van Hasselt, UMMZ 100592
Epinephelus adscensionis (Osbeck), UMMZ 174392
E. analogus Gill, UMMZ 173657
E. drummondhayi Goode & Bean, ANSP 74872
E. flavolimbatus Poey, USNM 171195
E. guaza (Linnaeus), MCZ 10196
E. guttatus (Linnaeus), UMMZ 176613
E. itajara (Lichtenstein), UMMZ 155054
E. morio (Valenciennes), UMMZ 139276
E. nigritus (Holbrook), USNM 134891
E. niveatus (Valenciennes), USNM 77786
E. striatus (Bloch), UMMZ 65315
Gonioplectrus hispanus (Cuvier), UMMZ 171874
Grammistes sexlineatus (Thunberg), UMMZ 100442
Mycteroperca bonaci (Poey), UMMZ 176007
M. interstitialis (Poey), UMMZ 176046
M. microlepis (Goode & Bean), UMMZ 87953
M. olfax (Jenyns), USNM 107066
M. phenax Jordan & Swain, UMMZ 172586
M. rubra (Bloch), MCZ 10138
M. tigris (Valenciennes), UMMZ 176138
M. venenosa (Linnaeus), UMMZ 176626
M. xenarcha Jordan, USNM 128757
Paranthias furcifer (Valenciennes), UMMZ 176629
Petrometopon cruentatum (Lacépède), UMMZ 172576
Rypticus nigripinnis Gill, UMMZ 171919
R. saponaceus (Bloch & Schneider), UMMZ 172625

Formula 0–0–2–:

Banjosidae: *Banjos banjos* (Richardson), UMMZ 176786
Branchiostegidae: *Branchiostegus japonicus* (Houttuyn), UMMZ 142740
Caulolatilis princeps (Jenyns), UMMZ 64141
Chaetodontidae: *Pomacanthus arcuatus* (Linnaeus), UMMZ 172867
Histiopteridae: *Quinquarius japonicus* (Döderlein), UMMZ 176815
Lethrinidae: *Pentapus caninus* (Cuvier), UMMZ 100207
Nemipteridae: *Scolopsis ciliata* (Lacépède), UMMZ 100285
S. margaritifera (Cuvier), UMMZ 100302
S. trilineata Kner, UMMZ 100218
Plesiopidae: *Plesiops melas* Bleeker, UMMZ 100294
P. nigricans (Rüppell), UMMZ 176824
Scatophagidae: *Scatophagus argus* (Linnaeus), UMMZ 171726

Serranidae: *Centrogenys vaigiensis* (Quoy & Gaimard), UMMZ 100361
Dules auriga Cuvier, UMMZ 95482
Niphon spinosus Cuvier, UMMZ 142707

Formula 0–0–0–1–:

Carangidae: *Alectis ciliaris* (Bloch), UMMZ 176802
A. indica (Rüppell), UMMZ 176767
Caranx speciosus (Forskål), UMMZ 176769
Elegatis bipinnulatus (Quoy & Gaimard), UMMZ 176768
Hemicaranx amblyrhynchus (Cuvier), UMMZ 155065
Naucrates ductor (Linnaeus), UMMZ 111113
Centrarchidae: *Acantharchus pomotis* (Baird) UMMZ 114419
Ambloplites rupestris (Rafinesque), UMMZ 171124-S
Chaenobryttus gulosus (Cuvier), UMMZ 166024
Enneacanthus chaetodon (Baird), UMMZ 144574
E. obesus (Girard), UMMZ 126725
Lepomis cyanellus Rafinesque, UMMZ 135601
L. humilis (Girard), UMMZ 175472
L. macrochirus Rafinesque, UMMZ 77982
Micropterus dolomieui Lacépède, UMMZ 171123-S
M. salmoides (Lacépède), UMMZ 139859
Cichlidae: *Cichlasoma salvini* (Günther), UMMZ M59-43
Paraneetroplus bulleri Regan, UMMZ M59-43
Menidae: *Mene maculata* (Bloch & Schneider), UMMZ 100338
Monodactylidae: *Monodactylus argenteus* (Linnaeus), UMMZ 176755
Pempheridae: *Pempheris schomburgki* Müller & Troschel, UMMZ 172775
Percichthyidae: *Percichthys trucha* (Valenciennes), UMMZ 61996
Pomatomidae: *Pomatomus saltatrix* (Linnaeus), UMMZ 109865
Serranidae: *Lateolabrax japonicus* (Cuvier), UMMZ 167424
Psammoperca waigiensis (Cuvier), UMMZ 100489
Rhegma bermudensis Kanazawa, UMMZ 176527
Siniperca chuatsi (Basilewski), UMMZ 167378
Sillaginidae: *Sillago sihama* (Forskål), UMMZ 176783
Theraponidae: *Datnia plumbea* Kner, UMMZ 100254

Formula 0–0–0–2–:

Acropomatidae: *Acropoma japonicum* Günther, UMMZ 142692
Apogonidae: *Apogon lineatus* Temminck & Schlegel, UMMZ 160823
Carangidae: *Alectis indica* (Rüppell), UMMZ 176767
Caranx latus Agassiz, UMMZ 167482
C. lundini (Jordan & Seale), UMMZ 56678
C. marginatus Gill, UMMZ 172034
C. uraspis Günther, UMMZ 176807
Chloroscombrus chrysurus (Linnaeus), UMMZ 174011
Decapterus punctatus (Agassiz), UMMZ 174059
Megalaspis cordyla (Linnaeus), UMMZ 70348

Selene vomer (Linnaeus), UMMZ 132812
Seriola zonata (Mitchill), UMMZ 86220
Trachurus lathami Nichols, UMMZ 174001
Centrarchidae: *Archoplites interruptus* (Girard), UMMZ 129601
Centrarchus macropterus (Lacépède), UMMZ 163844
Enneacanthus chaetodon (Baird), UMMZ 144574
E. gloriosus (Holbrook), UMMZ 138485
E. obesus (Girard), UMMZ 126725
Centropomidae: *Centropomus viridis* Lockington, UMMZ 161630
Chaetodontidae: *Chaetodon triangulus* Cuvier, UMMZ 100511
Drepanidae: *Drepane punctata* (Linnaeus), UMMZ 100457
Emmelichthyidae: *Erythrocles schlegeli* Richardson, UMMZ 176789
Ephippidae: *Chaetodipterus faber* (Broussonet), UMMZ 164875
Gerridae: *Diapterus mexicanus* (Steindachner), UMMZ 143689
D. plumieri (Cuvier), UMMZ 172748
Eucinostomus argenteus Baird & Girard, UMMZ 136511
E. gula (Cuvier), UMMZ 113256
E. havana (Nichols), UMMZ 105699
E. lefroyi (Goode), UMMZ 172378
Gerres cinereus (Walbaum), UMMZ 161506
G. japonicus Bleeker, UMMZ 176796
G. macracanthus Bleeker, UMMZ 176762
G. punctatus Cuvier, UMMZ 100456
Pentaprion longimanus, UMMZ 176760
Girellidae: *Girella nigricans* (Ayres), UMMZ 63508
Kuhliidae: *Kuhlia malo* (Valenciennes), UMMZ 56681
K. marginata (Cuvier), UMMZ 100455
Kyphosidae: *Kyphosus sectatrix* (Linnaeus), UMMZ 172592
Labracoglossidae: *Labracoglossa argentiventris* Peters, UMMZ 142717
Lethrinidae: *Lethrinus haematopterus* Schlegel, UMMZ 142718
Lobotidae: *Datnioides microlepis* Bleeker, UMMZ 177263
Lobotes surinamensis (Bloch), UMMZ 168936
Lutjanidae: *Lutjanus griseus* (Linnaeus), UMMZ 172329
Mullidae: *Mulloidichthys martinicus* (Cuvier), UMMZ 172596
Nandidae: *Polycentrus schomburgki* (Müller & Troschel), UMMZ 108907
Pristolepis fasciatus (Bleeker), UMMZ 70701
Nemipteridae: *Gymnocranius griseus* (Schlegel), UMMZ 176780
Oplegnathidae: *Oplegnathus fasciatus* (Temminck & Schlegel), UMMZ 142727
O. punctatus (Temminck & Schlegel), UMMZ 176816
Platacidae: *Platax orbicularis* (Forskål), UMMZ 100434
Pomadasyidae: *Bathystoma rimator* (Jordan & Swain), UMMZ 147756
Haemulon plumieri (Lacépède), UMMZ 172973
Hapalogenys maculatus Richardson, UMMZ 176792
H. mucronatus (Eydoux & Souleyet), UMMZ 176805
Pomadasys bayanus Jordan & Evermann, UMMZ 172140
P. crocro (Cuvier), UMMZ 172792
P. hasta (Bloch), UMMZ 176774

Plectorhinchus cinctus (Temminck & Schlegel), UMMZ 176791
P. lineatus (Cuvier), UMMZ 100238
Pomatomidae: *Scombrops boops* (Houttuyn), UMMZ 176779
Sciaenidae: *Aplodinotus grunniens* (Rafinesque), UMMZ 166978
Argyrosomus argenteus (Houttuyn), UMMZ 176753
Leiostomus xanthurus Lacépède, UMMZ 165091
Pogonias cromis (Linnaeus), UMMZ 139384
Scorpidae: *Medialuna californiensis* (Steindachner), UMMZ 130678
Microcanthus strigatus (Cuvier), UMMZ 176795
Serranidae: *Acanthistius patachonicus* (Jenyns), UMMZ 95473
Centropristes ocyurus (Jordan & Evermann), UMMZ 174056
C. philadelphicus (Linnaeus), UMMZ 129887
C. striatus (Linnaeus), UMMZ 136590
Chelidoperca hirundinacea (Valenciennes), UMMZ 142690
Diplectrum formosum (Linnaeus), UMMZ 136555
Doderleinia berycoides (Hilgendorf), UMMZ 142702
Hypoplectrus unicolor (Walbaum), UMMZ 176389
Polyprion americanus (Bloch and Schneider), USNM 39879
Prionodes baldwini Evermann and Marsh, UMMZ 174349
P. phoebe (Poey), UMMZ 176431
P. tabacarius Cuvier, UMMZ 172575
P. tigrinus (Bloch), UMMZ 174393
Roccus americanus (Gmelin), UMMZ 126991
R. chrysops (Rafinesque), UMMZ 171119
Serranus beta Hildebrand, UMMZ 174151
S. dewegeri Metzelaar, UMMZ 174570
S. hepatus (Linnaeus), UMMZ 61421
Serranellus subligarius (Cope), UMMZ 153450
Stereolepis gigas Ayres, UMMZ 94693
Sparidae: *Calamus penna* (Valenciennes), UMMZ 153968
Oblada melanura (Linnaeus), UMMZ 173691
Theraponidae: *Therapon jarbua* (Forskål), UMMZ 100566
T. theraps Cuvier, UMMZ 176758

Formula 0–0–0–3–:

Centrarchidae: *Enneacanthus gloriosus* (Holbrook), UMMZ 138485
Ephippidae: *Chaetodipterus faber* (Broussonet), UMMZ 145928

Formula 0–0–0–0–1–:

Bramidae: *Brama rayi* (Bloch), UMMZ 97195
Carangidae: *Parona signata* (Jenyns), UMMZ 95463
Trachinotus falcatus (Linnaeus), UMMZ 143182
Toxotidae: *Toxotes jaculatrix* (Pallas), UMMZ 171838

Formula 0–0–0–0–0–1–:

Carangidae: *Oligoplites saurus* (Bloch and Schneider), UMMZ 153972

Formula 0–0–0–0–0–0–1–:

Carangidae: *Vomer setapinnis* (Mitchill), UMMZ 166075
Centrarchidae: *Pomoxis annularis* Rafinesque, UMMZ 81219
P. nigromaculatus (LeSueur), UMMZ 146780

Formula 0–0–0–0–0–0–2–:

Centrarchidae: *Pomoxis nigromaculatus* (LeSueur), UMMZ 146780

Formula 0–0–0–0–0–0–0–1–:

Centrarchidae: *Pomoxis annularis* Rafinesque, UMMZ 81219
P. nigromaculatus (LeSueur), UMMZ 146780

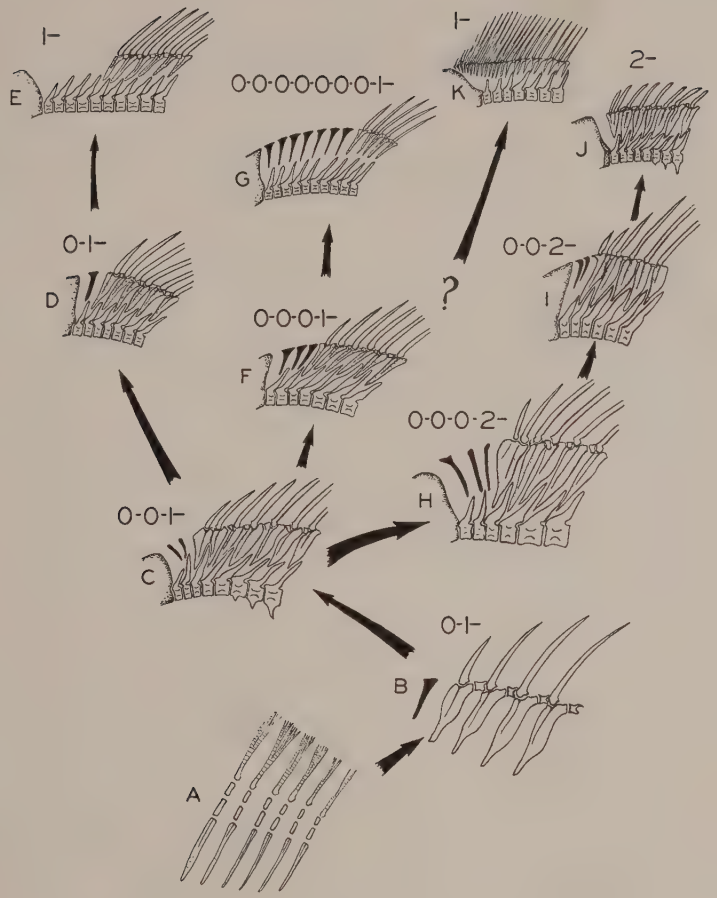

PLATE I

Some Evolutionary Trends in Dorsal-Fin Supports

Figs. *A* and *B* are hypothetical ancestral types. All other figures are based on X-ray photographs of specimens as follows: *C. Alphestes afer*, UMMZ 176033, 235 mm., Bermuda; *D. Perca fluviatilis*, UMMZ 159289, 116 mm., Czechoslovakia; *E. Percina caprodes*, UMMZ 158976, 75 mm., Maryland; *F. Datnia plumbea*, UMMZ 100254, 100 mm., Philippine Islands; *G. Pomoxis annularis*, UMMZ 171125-S, 192 mm., Lake St. Clair, Ontario; *H. Hypoplectrus unicolor*, UMMZ 176389, 80 mm., Bermuda; *I. Scatophagus argus*, UMMZ 171820, 115 mm., Java; *J. Priacanthus cruentatus*, UMMZ 172731, 161 mm., Puerto Rico; *K. Coryphaena hippurus*, UMMZ H29-175, 260 mm., Korea. The fishes illustrated are selected to indicate trends in the character of the dorsal-fin supports; phylogenetic continuity of the examples used is not implied.

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MAN AND THE CHANGING FISH FAUNA OF THE AMERICAN SOUTHWEST[1]

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The past 100 years have witnessed drastic changes in the rivers of western North America and in their fish faunas. Deterioration of stream flow has greatly shrunk the ranges of many species, and other species have been denied access to large segments of their original distribution by the construction of barrier dams. Profound modification of pristine environments has restricted habitable waters, and the introduction and establishment of a host of exotics have brought about replacement as well as reduction of native forms through competition, predation, and hybridization. Some species and subspecies have become extinct, and many others are endangered (Matthiessen, 1959). These changes have been particularly marked in areas of restricted water supply such as characterize the arid Southwest (Fig. 1). Much of this region is embraced by the Basin and Range Province (Fenneman, 1931, pl. I), including the Great Basin, Sonoran Desert, and the Chihuahuan Desert of northern Mexico.

Only about 100 species of strictly fresh-water fishes are known west of the Rocky Mountains and north of Mexico—a depauperate fauna characterized by relicts, monotypic genera, and much regional

[1] The initial version of this paper was presented at the Fifth Annual Symposium on Systematics, Missouri Botanical Garden, St. Louis, on October 25, 1958, under the general subject "Taxonomic Consequences of Man's Activities." Field work has been generously supported by the Horace H. Rackham School of Graduate Studies and the Museum of Zoology, University of Michigan. Space prohibits naming the many ranchers, old-timers, colleagues, and officials to whom I am deeply indebted for historical testimony and other assistance. Credit to some of these people is given in the text. Permits to collect in Arizona, California, Nevada, New Mexico, Texas, and Utah were kindly arranged by the authorities of those states. The map (Fig. 1) was lettered by W. L. Brudon.

The following museum abbreviations are used: CAS, California Academy of Sciences; MCZ, Museum of Comparative Zoology, Harvard College; SU, Stanford University Natural History Museum; UMMZ, University of Michigan Museum of Zoology; and USNM, United States National Museum.

FIG. 1. Drainage map of Southwestern North America, showing localities mentioned in the text.

endemism (Miller, 1959). Many of the species have limited ranges, and some are even confined to habitats that contain only a few thousand gallons of water or cover scarcely an acre. Presumably as a result of greatly reduced competition and little pressure from predation, these isolated populations lack the defense mechanisms that are developed in more nearly saturated faunas, and hence they have been rather easy prey for the typically more aggressive exotic species.

It is the purpose of this contribution to describe some of the environmental modifications that have occurred in the Southwest, to document where possible the changing nature of the fish fauna, and to present evidence that modern man has been the chief architect of these changes.

Habitat Changes

The aboriginal habitats have become modified in various ways. There has been a shift from clear, dependable streams to those of intermittent flow subject to flash floods that carry heavy loads of silt. As a result of loss in volume and destruction of vegetation, there has been a trend toward rising temperatures in the surviving waters. The smaller creeks, springs, marshes, and lagoons have disappeared, due in part to severe lowering of the water table. There has been destruction of trees, grasses, and aquatic plants; pollution from industrial and domestic wastes; deep channeling (arroyo cutting) of stream beds; and gully erosion on bare hillsides. Examples of these types of modifications are considered in this section.

Colorado River Basin in Arizona

Lower Colorado River.—The lower Colorado River, from the Lake Mead area to the Gulf of California, flows through a desert region of low plains and narrow valleys broken by short mountain groups. The source of nearly all of its water is in the high mountains of the upper basin. In its natural condition the river was swift, silt-laden, and subject to spectacular fluctuations in volume and turbidity, annually carrying thousands of tons of silt into the Gulf of California. Its maximum flow usually was attained in June, diminished greatly in August, and was very low from September to February. At Yuma, Arizona, a peak flow of 250,000 c.f.s. occurred in 1916 and a minimum daily flow of only 18 c.f.s. was recorded in the drought year of 1934 (Dill, 1944, p. 123). With the completion of Hoover Dam in 1935, control of the river began. The succession of dams lying between Lake Mead and Yuma has transformed the Colorado into a series of deep, placid reservoirs with connecting channels of clear water and regulated volume. The water temperature has been strikingly modified. Originally it varied from about 50° to 90° F. or more annually. Now, below Hoover Dam and Davis Dam the fluctuation is from 54° to 62° F., providing temperatures suitable for the development of an important trout fishery. Below Parker Dam, however, the water is clear but warm. Dredging of the river channel has further modified aquatic habitats by the elimination of marshes, lakes, and sloughs and by producing a straight sluice that is poor in food and cover and with waters of relatively high turbidity (Beland, 1953a). Introduction of

a host of exotic species has had a striking effect on the original biota (Tab. I).

Gila River.—This river, rising in western New Mexico and following a westerly course of more than 500 miles to its junction with the Colorado River at Yuma (Fig. 1), has changed drastically since it was first seen by white men. In Arizona, it once was a large, essentially permanent stream of clear to "sea-green" water, with a well-defined, narrow channel flanked by numerous cottonwoods and set off by a dense growth of willows and cane that rendered it difficult of approach. Along its course were numerous lagoons and extensive marshes that abounded in waterfowl, beaver, and fish life (Parke, 1857, pl. IV opp. p. 19; Antisell, 1857, pp. 134–135). On November 17, 1846, Emory (1848, p. 91) wrote of the Gila (when he was perhaps 35 or 40 miles west of Gila Bend): "The bottoms of the river are wide, rich, and thickly overgrown with willow and a tall aromatic weed, and alive with flights of white brant, geese, and ducks, with many signs of deer and beaver." Prior to 1920, these same bottom lands had become "desolate wastes of sand and silt" (Ross, 1923, p. 66). Throughout most of its channel, the river is now largely intermittent, and in its lower 250 miles, from east of Florence to Yuma, it is normally completely dry; its trees and marshes and once abundant aquatic life have long since disappeared. The condition of surface waters in the Gila River basin, Arizona, in 1950 is shown on a map by Miller (1954).

In October 1849, the river was negotiated from the Pimas Villages (south of Phoenix) to its mouth by a flatboat 16 feet long and 5½ feet wide, carrying a family and 2 other men. During the winter of 1890, Stanley Sykes and a partner, on a dare, attempted to go by boat over this same route. By dragging their flat-bottomed craft over frequent sand bars and across numerous dry stretches (for even then the river had become intermittent in midwinter), they finally reached Yuma after a 30-day struggle—undoubtedly the last men to traverse the lower Gila by boat (Sykes, personal interview, 1950).

Although the pristine watershed of the Gila River did much to regulate the runoff, the Gila, even in its earlier days (1833–69), was not without occasional floods—probably resulting from rains of unusually long duration. The effect of these, however, was to spread out over wide areas rather than to become great detritus-carrying, eroding flood crests such as have occurred subsequent to settlement by the

white man (Olmstead, 1919, p. 9). As the river changed, it entrenched itself in its upper reaches and cut away much of the former flood plain, whereas in its lower course (below the mouth of the Santa Cruz River) the original well-marked channel soon became filled by flood deposits to form a broad, sandy plain (Bryan, 1925, pp. 342–343). In 1875, the well-defined channel of the Gila River near Solomonsville (in T. 7 S., R. 27 E.) had an average width of 138.6 feet and included an area of 103.57 acres, whereas by 1916 the same length of channel averaged more than 1,900 feet wide and occupied an area of 1,503 acres (Olmstead, 1919, p. 11).

San Pedro River.—This stream (Fig. 1) was originally the only permanent southern tributary of the Gila River. In 1870 its nearly level valley had a narrow, grassy bed with banks that were well clothed with vegetation. There was an abundance of willow, cottonwood, sycamore, and ash trees, with excellent growths of grasses (sacatón and grama). Beaver dams retarded the heavy summer rains and prevented channel cutting. Ciénegas, such as the one near the mouth of the then perennial Babocomari River (Dipeso, 1951, p. 3), were common. In the 1600's, more than 2,000 aborigines lived in 15 villages along the lush San Pedro Valley below Fairbank (Dipeso, 1951, p. 7). By 1892 or 1893, however, a gully 3 to 20 feet deep had been cut for 125 miles, and by 1900, the river had entrenched its bed from 10 to 40 feet; trees and underbrush had been destroyed or greatly reduced, the grasses were largely gone, and cattle and horses, moving from feed to water, had cut numerous erosion channels from the hills to the river (Bryan, 1925, p. 342; Thornthwaite et al, 1942, p. 103). In its original condition, the San Pedro was of sufficient size and volume to support a relatively large and varied fish fauna (Tab. II).

San Simon Valley.—This valley is in southeastern Arizona and the adjacent part of New Mexico, and extends north-northwestward for 85 miles from the head of San Bernardino Valley (20 miles north of the International Line) to the Gila River at Solomon (formerly Solomonsville), just east of Safford. The often heavy summer storms were restrained in the valley by the extensive flats of sacatón, and the water sank into the unbroken meadow to furnish an artesian supply near the central part of the valley. According to Olmstead (1919, p. 79) about 1883, "certain settlers near Solomonsville whose lands were along this drainage line were annoyed at finding occasionally after heavy rains that sand and detritus had been washed down on them

from the San Simon. They accordingly excavated a small channel, about 4 feet deep and 20 feet wide, for a short distance so that the floods could be discharged in concentrated flow into the Gila. They also built funneling levees so that there would be no question of the water reaching this artificial trough. It worked, and today there is a chasm, in many places 600 to 800 feet wide and from 10 feet to 30 feet deep, for 60 miles, as the indirect result of their effective work to protect their lands from overflow." Efforts by the Soil Conservation Service finally checked the headward erosion of San Simon Creek just short of its drainage of the ciénega that lies along the Arizona-New Mexico line. The erosion has produced deep and wide gullies, permanently changing the surface over most of the length of the valley.

Blue River.—This stream is a mountain tributary of the San Francisco River, which joins the Gila River below Clifton in eastern Arizona (Fig. 1). In 1885 or 1886, the floor of the canyon of Blue River was well sodded and covered with grama grass, hardwoods, and pine. The stream supported many native trout, *Salmo gilae* (Miller, 1950). The valley had an average width of 700 feet, was well settled, and was nearly all under cultivation. In 1900, floods began to incise and widen the channel and a regime of active erosion was well under way by 1906. By 1916, the valley bottom had been converted into a wide wash and was ruined for agriculture as well as for pasturage; less than 8 per cent of the original arable area then remained (Olmstead, 1919, p. 68; Bryan, 1925, p. 342).

Little Colorado River.—This river rises on the northern slopes of the White Mountains of eastern Arizona and flows north and westward to its junction with the Colorado River at the head of Grand Canyon (Fig. 1). In the middle of the sixteenth century, the Little Colorado was described as a "... fine, beautiful, and selected river almost as large as the Del Norte, containing many groves of poplars and willows." It was named the Río Alameda, meaning the river of groves, in reference to the great groves of cottonwoods that lined much of its course (Colton, 1937). In 1851 there were extensive swamps above Winslow (Sitgreaves, 1853, pp. 7–8), and at about the same time Whipple (1856, pp. 30–31) wrote as follows: "The river is about 30 feet wide flowing between alluvial banks eight to ten feet in height.... The banks of the main stream ... are sprinkled with cot-

ton-wood trees . . . the river-bottom is in some places marshy, with willow thickets, and in others covered with a loose, pulverized soil." In the 1880's the river, shortly above Grand Falls (about 35 miles northeast of Flagstaff), was a narrow perennial stream, and its banks were bordered by a fine stand of old and young cottonwoods. Many beavers were supported by an ample food supply in the young cottonwood trees. Grama grass covered the adjacent hills. Today, the Little Colorado is normally dry between Grand Falls and Winslow, the trees have long since disappeared, and the fine grass has vanished. When the river does flow between Holbrook and Winslow, it is through a wide, treeless valley, where its bed is broad and sandy, its banks deeply entrenched, and vegetation is scarce. Since around the turn of the century, disastrous floods have converted its sandy bed into a raging, eroding torrent, heavily laden with silt.

OTHER AREAS

Southern California.—The major coastal valley is a complex lowland that lies at the southern base of the San Gabriel and San Bernardino ranges, opens directly westward to the Pacific, and communicates with the Mohave and Colorado deserts via Cajon and San Gorgonio passes. Its total area is about 3,000 square miles. Three major streams traverse this valley, herein called the Los Angeles Plain: the Santa Ana, the San Gabriel, and the Los Angeles. Of these, the Santa Ana River is the largest. It rises high in the San Bernardino Mountains and flows to the Pacific through 2 canyons on the plains, an upper (about 50 miles west of its source) and a lower (through the Santa Ana Mountains); its total length is about 100 miles. The utilization of this river by man is indicated by the following statement: "Probably no other stream of its size in the United States is made to serve greater or more varied uses" (McGlashan, 1930, p. 176). West of the Santa Ana is the San Gabriel River, with a total length of about 70 miles; its headwaters rise on the western flank of Mount San Antonio (Old Baldy) and from the southern slopes of other high peaks. The Los Angeles River originates to the northwest of the city in several small tributaries which normally sink into the sands of San Fernando Valley. Impervious rocks at the lower end of this valley force the underground water to the surface, and the river originally flowed from this point through a valley of low, rolling hills to the

Pacific near Long Beach, although the last 10 miles of its channel were normally dry. The river is joined in Los Angeles by Arroyo Seco, rising on the mountain slopes north of Pasadena.

Utilization of the waters of these rivers for irrigation began as early as 1821 but extensive use for that purpose did not commence until the 1880's. Before the advent of man, the waters of the mountain streams feeding these rivers promptly sank into the alluvial plains, except during periods of unusually great and prolonged rainfall. Below their headwater region, however, the rivers reappeared as perennial surface flows wherever there was an impervious barrier like the bedrock obstructions in the Santa Ana River near Riverside and in Santa Ana Canyon. Between about 1875 and 1905, however, practically all of the normal flow of these streams was appropriated for irrigation purposes. Extensive moist lands about San Bernardino, numerous springs, and large ciénegas also disappeared as the water supply was drained away by pumping plants and artesian wells. At a time preceding the settlement of San Jose Valley (near Pomona), San Jose Creek was a summer stream fed by waters rising as springs in the old Palomares Ciénega; after settlement the ciénega disappeared and the valley was deprived of its normal water source (Mendenhall, 1908, p. 55). In aboriginal times probably 50 to 75 per cent of the stream courses within the basins of the 3 major rivers afforded permanent habitats for aquatic organisms; very probably the lower parts of all 3 rivers were normally dry or intermittent most of the year. At present, the perennial surface flow of these streams has been reduced to a fraction of what it was in 1850.

Upper Río Grande.—In the early 1900's the Río Grande had a rather small but permanent flow in its upper part, southward about to the vicinity of Albuquerque; but from there to the Texas border it often went dry in years of below normal rainfall or toward the close of the dry season. The river was described as "essentially a storm-water stream, subject to great and sudden floods" (Lee, 1907, p. 7). Río Puerco, an important tributary from the west, already had developed local gullies during the period from 1846 to 1877, with trenches up to 30 feet deep and 100 feet wide (Antevs, 1952, p. 379). That the upper Río Grande was once a larger river of more reliable flow is indicated by the record of a sturgeon taken near Albuquerque in the 1870's and the identification of remains of the blue sucker (*Cycleptus elongatus*) from an Indian site west of Santa Fe which

dates from about 1500 (Cope and Yarrow, 1875, p. 639; Gehlbach and Miller, 1961; see also Henderson and Robbins, 1913).

Fish Faunal Changes

Fish faunas have undergone considerable alteration in the American Southwest but documentary evidence of these changes has not heretofore been available. Depletion has been widespread, many species are threatened with extermination, and others have already become extinct. The introduction of a large number of alien species into a generally depauperate fauna has resulted in species replacement in many waters, especially in the larger impoundments.

documentary evidence for colorado river system

The most impressive documentation for a changing fish fauna pertains to southern Arizona, where repeated collections spanning a century provide a progressive record of the change (Tab. I–III). This record dramatically demonstrates the sharp decline in native fishes. In many places, notably the lower Colorado River, introduced kinds are now flourishing. The data are taken from the observations and records of the explorations during the middle of the nineteenth century (principally from the Pacific Railroad Survey reports), the accounts by Gilbert and Scofield (1898) and Snyder (1915), the unpublished data (1904) of F. M. Chamberlain,[2] the records and specimens (accumulated since 1926) in the Museum of Zoology, University of Michigan, and the data presented by Dill (1944). In addition to the progressive change shown for single stations, there is also the picture obtained from the testimony of old-timers as to the former occurrence, distribution, and abundance of fishes now nearing extinction. Testimony of this nature was particularly sought by me during a 2½-month survey of Arizona in the spring of 1950.

colorado and gila rivers, yuma (table i)

The primitive fish fauna of the Colorado River near Yuma evidently comprised very few species. The huge Colorado squawfish, *Ptychocheilus lucius* Girard, the bonytail, *Gila robusta elegans* Baird and Girard, and the humpback sucker, *Xyrauchen texanus* (Abbott), are the only fishes mentioned in the early surveys, and they are the

[2] Deposited in the Division of Fishes, U. S. National Museum, Washington, D. C.

TABLE I

A Century of the Fish Fauna in the Colorado and Gila Rivers Near Yuma, Arizona

Parentheses around a cross indicate that the species, although not reported or taken, was probably present. R = rare. Collections from Gila River were made at its mouth and 8 to 10 miles above (at or near Dome).

Species	1854	1890–95	1904	1926	1940–42	1950–55
Native species:						
Elops affinis	—	—	—	—	×	×
*Gila robusta elegans**	×	×	×	×	R	—
Ptychocheilus lucius	×	×	×	×	R	—
Plagopterus argentissimus	(×)	×	—	—	—	—
Catostomus latipinnis	(×)	—	—	—	—	—
Xyrauchen texanus	×	×	×	×	R	—
Cyprinodon macularius	(×)	×	(×)	×	—	—
Poeciliopsis occidentalis	(×)	×	(×)	×	—	—
Mugil cephalus	—	—	—	—	×	×
Introduced species:						
Dorosoma petenense	—	—	—	—	—	×
Cyprinus carpio	—	×	×	×	×	×
Notropis lutrensis	—	—	—	—	—	×
Ictalurus punctatus	—	—	—	—	×	×
I. melas	—	—	×	×	×	×
I. natalis	—	—	—	—	×	×
Gambusia a. affinis	—	—	—	×	×	×
Micropterus salmoides	—	—	—	—	×	×
Lepomis cyanellus	—	—	—	×	×	×
L. macrochirus	—	—	—	—	×	×
Pomoxis spp. (2)	—	—	—	—	×	×
Total species:						
Native	7	6	5	5	5	2
Exotic	0	1	2	4	10	12

* *Gila r. robusta* was taken at Dome (Gila River) during 1892–94.

only ones that have been collected from the river at Yuma. However, the flannelmouth sucker, *Catostomus latipinnis* Baird and Girard, must have once inhabited the main river since it occurs in both the Gila River drainage and in the middle and upper parts of the Colorado River basin; hence I have added it to the list. The fate of the squawfish is discussed later (p. 392).

Between 1890 and 1895 the woundfin, *Plagopterus argentissimus* Cope (Miller and Hubbs, 1960), was present in the Gila River at its mouth (Gilbert and Scofield, 1898, p. 496). Other species listed in Table I that were taken only in the lower Gila include the desert pupfish, *Cyprinodon macularius* Baird and Girard, and the Gila topminnow, *Poeciliopsis occidentalis* (Baird and Girard). That the habitat in the lower Gila River was very favorable for these quiet-water species is indicated in the report by Antisell (1857, p. 133), which describes how the river spread broadly and was in places swampy and overgrown with willows. The appearance of the euryhaline striped mullet, *Mugil cephalus* Linnaeus, around 1934–35, and of the machete or ten-pounder, *Elops affinis* Regan, in 1941 (Glidden, 1941), is plausibly attributed to the disappearance of the predatory Colorado squawfish and likely also to other ecological changes, such as the advent of clear water and a relatively stable flow. A number of the exotic species represent intentional introductions or bait releases (Miller, 1952; Hubbs, 1954; Kimsey, Hagy, and McCammon, 1957; Shapovalov, Dill, and Cordone, 1959, p. 166), and still other introduced forms may now occur in the Colorado around Yuma (Beland, 1953b; St. Amant, 1959). The recent record (Hubbs, 1953) of *Eleotris picta* Kner and Steindachner from a canal spillway north of Yuma is not included in the tabulation since this specimen obviously represents a rare straggler; the species has not been taken from the Colorado River, and there have been no subsequent records from the lower Colorado River basin.

SAN PEDRO RIVER (TABLE II)

In 1846 the Colorado squawfish was reported to have run up the San Pedro River to about Fairbank (Fig. 1), and remains of this species have been recovered from an archaeological site along this river at nearby Quiburi (Miller, 1955, pp. 133–134); the trash heap containing the fishbones was dated as A.D. 1704–63. Humpback suckers also once inhabited the San Pedro for they were reported by Chamberlain to have been marketed at Tombstone as "buffalo," probably prior to the 1880's (Miller, 1955, p. 134). The desert pupfish, described from the San Pedro River near Benson, evidently inhabited the then marshy canyon just below (Leopold, 1951, p. 310), but has not since been collected from the Arizona part of that river. The species was taken, however, 100 years after its original capture, in

TABLE II

CHANGING FISH FAUNA OF SAN PEDRO RIVER, BETWEEN BENSON AND FAIRBANK, ARIZONA, 1846–1950*

R = rare.

Species	1846–1854	1904	1939	1950
Native species:				
Gila robusta	×	×	—	—
Ptychocheilus lucius	×	—	—	—
Rhinichthys osculus	×	R	—	—
Agosia chrysogaster	×	×	×	×
Tiaroga cobitis	×	×	×	×
Meda fulgida	×	×	×	×
Catostomus insignis	×	×	×	—
C. latipinnis	×	—	—	—
Pantosteus clarki	×	×	×	—
Xyrauchen texanus	×	—	—	—
Cyprinodon macularius	×	—	—	—
Introduced species:				
Ictalurus melas	—	—	×	—
Lepomis cyanellus	—	—	×	—
Total species:				
Native	11	7	5	3
Exotic	0	0	2	0

* In 1959 (June) the river was dry, or damp only, in this section but it was flowing farther upstream at Charleston (about 10 miles above Fairbank); here the river contained all the native fishes listed for 1939.

the Mexican part of the San Pedro in the spring of 1950 (UMMZ 162680).

It is noteworthy that the species of Arizona that persists longest in the dwindling waters of sandy streams, the longfin dace (*Agosia chrysogaster* Girard), still survives in the many shallow, intermittent Arizona streams, and was by far the commonest fish in the upper San Pedro River in June 1959. The fishes that have disappeared from the lower part of the stream are those that either require pools (*Gila, Catostomus, Pantosteus*), long since filled with sand, or a sizable, permanent river with strong current (*Ptychocheilus, Xyrauchen*); the desert pupfish presumably utilized marshy areas that must have been drained rapidly with the onset of arroyo cutting in 1883 (Bryan,

1925, p. 342). The speckled dace, *Rhinichthys osculus* (Girard), was perhaps eliminated chiefly by rising water temperatures as the river became deeply entrenched, the vegetation was destroyed, and the water supply shrank. The flow diminished so markedly between 1939 and 1950 that even the two exotic species, the black bullhead (*Ictalurus melas* Rafinesque) and the green sunfish (*Lepomis cyanellus* Rafinesque), had disappeared here, presumably because of insufficient cover. On June 22, 1959, the river was dry at Benson, and only damp at St. David and Fairbank.

SALT RIVER (TABLE III)

The shift from 11 native species to 5 exotic species in the Salt River south of Phoenix, during approximately a half century, reflects changing water conditions upstream (dam construction, irrigation) and the establishment of exotics. Before the turn of the century the river was of sufficient size and flow to support such big-river or current-loving fishes as the roundtail (*Gila r. robusta* Baird and Girard), bonytail (*G. r. elegans*), woundfin (*Plagopterus*), flannelmouth sucker (*Catostomus latipinnis*), and humpback sucker (*Xyrauchen*); overflow, marshlike areas presumably provided habitats for the pupfish and topminnow (*Cyprinodon* and *Poeciliopsis*). As the river dwindled in volume and depth to a comparatively shallow stream dominated by shifting sand, longfin dace (*Agosia*) appeared and attained numerical superiority, and *Gila robusta intermedia* Girard, a headwater and small-creek ecotype, appeared in place of the bonytail. With the desiccation of the river at this point by 1943, only predatory introduced species remained.

Farther upstream in Salt River, at and near the present site of Roosevelt Dam, there were, in 1904, only 1 exotic species (the carp), and 10 native species including Colorado squawfish, spikedace (*Meda fulgida* Girard), flannelmouth and humpback suckers, and the Gila topminnow. By 1937, *Meda* had disappeared, the last adult squawfish was captured, the humpback sucker had vanished, and *Poeciliopsis* had been eliminated. The bigmouth buffalo (*Ictiobus cyprinellus*), yellow bullheads, bluegills, yellow perch, and yellow bass had become established—a total of 7 native and 6 exotic species. In 1950, the reservoir contained only 8 introduced fishes, although near its head Salt River still supported 6 native species, including roundtails,

TABLE III

MODIFICATION OF THE FISH FAUNA IN THE SALT RIVER NEAR TEMPE, ARIZONA, 1890–1944

Parentheses indicate probable occurrence.

Species	April–May 1890	Sept. 11 1926	1943–44*
Native species:			
Agosia chrysogaster	—	×	—
Gila robusta robusta	×	×	—
G. robusta intermedia	—	×	—
G. robusta elegans	×	—	—
Rhinichthys osculus	×	—	—
Meda fulgida	×	—	—
Plagopterus argentissimus	×	—	—
Catostomus insignis	×	—	—
C. latipinnis	×	—	—
Pantosteus clarki	×	—	—
Xyrauchen texanus	×	—	—
Cyprinodon macularius	(×)	×	—
Poeciliopsis occidentalis	×	×	—
Introduced species:			
Cyprinus carpio	—	—	×
Ictalurus melas	—	—	×
Gambusia a. affinis	—	×	×
Lepomis macrochirus	—	—	×
L. cyanellus	—	×	—
Pomoxis nigromaculatus	—	—	×
Total species:			
Native	11	5	0
Exotic	0	2	5

* These collections were made on December 1 and March 23, respectively, from a series of gravel pits in the river bed, which was otherwise dry.

speckled dace, *Catostomus insignis*, *C. latipinnis*, and *Pantosteus clarki* (Baird and Girard).

SANTA CRUZ RIVER BASIN

In Sonoita Creek, the only important eastern tributary of the Santz Cruz River between Tucson and Nogales, Arizona, Chamberlain collected, in April 1904, near Patagonia, *Agosia*, *Catostomus insignis*, *Pantosteus*, and *Poeciliopsis*. Joseph Mailliard obtained 2

specimens of *Cyprinodon macularius* there on September 20, 1927 (CAS 18561). In July 1928, C. E. Burt sampled the fishes at the same place and obtained all but *C. insignis* and *C. macularius* plus an additional species, the speckled dace. In September 1938, Carl L. Hubbs secured the same species taken by Burt. In April 1959, our party found the stream almost fishless, and took only *Agosia*. The creek exhibited obvious signs of severe erosion, and the area between Patagonia and Nogales showed clearly the effects of serious overgrazing, with impoverished and badly eroding soil. Many of the great cottonwoods along Sonoita Creek, and in the Santa Cruz River valley, above and below the mouth of that creek, had died—probably as a result of the drastic lowering of the water table that has been accelerated since 1950 by the swelling population in southern Arizona. The original stands of tall grass had long since been replaced by mesquite, cholla, prickly pear, and burroweed.

For many years the Santa Cruz River, intermittent from near Nogales almost to Tucson, rose to the surface shortly above San Xavier Mission, about 8 miles south of Tucson. Here, on March 29, 1904, Chamberlain obtained 5 species: *Agosia chrysogaster*, *Gila robusta intermedia*, *Catostomus insignis*, *Pantosteus clarki*, and *Poeciliopsis occidentalis*. By April 25, 1937, when Allan R. Phillips sampled this perennial flow, only the resistant *Agosia* remained, and this is the only species that I found there on July 12, 1939. By April 13, 1950, the flow had disappeared, and I was informed by Raymond Hock (then of the University of Arizona) that it went dry for the first time during the previous winter. Even in early historic time, the Santa Cruz ordinarily had no surface flow from some distance below Tucson to its confluence with Gila River. It formerly maintained a permanent flow in the headwaters, near Lochiel (Schwalen, 1942, pl. II), but pumping in the San Rafael Valley eliminated this surface water and its fishes (*Gila*, *Agosia*, *Poeciliopsis*) between 1950 and 1956 (C. H. Lowe, Jr., personal communication).

EXTINCT AND ENDANGERED SPECIES

Since the close of the nineteenth century, no fewer than 6 species, and probably 7, have become extinct in the American Southwest. At least 13 additional forms have either been locally exterminated or are threatened with depletion to levels from which they might not be able to recover. In the following discussion, extinct species are treated

first; some of the endangered forms are covered elsewhere in this report.

Stypodon signifer Garman, stumptooth minnow.—This unique genus and species was described from 2 specimens collected in 1880 in a spring on the Chihuahuan Desert near Parras, Coahuila, Mexico (Fig. 1). It is characterized by having distinctively shaped pharyngeal arches with the teeth molariform to bluntly pointed and reduced to only 3 on each arch. Aside from the types, I am aware of only one collection (USNM 50971, 4 poorly preserved specimens) taken by George Hochderfer in 1903, presumably from the type locality. In May 1953, Carl L. and Laura C. Hubbs made a determined effort to obtain the species but were unsuccessful. All testimony they obtained indicated that there no longer are any natural springs in the immediate vicinity of Parras or anywhere in the Parras basin or in the great desert basin to the north. The flow of the springs has been increased or maintained by tunneling into the lava hill from which they issue, but the flow is concentrated into a reservoir, from which it is diverted through ditches into a cotton mill and onto fields. The reservoir contains carp. The reduced flow in the stream bed is affected by industrial and domestic sewage. These modifications of the habitat have probably been responsible for the elimination of this species, as well as *Dionda episcopa punctifer* and *Cyprinodon latifasciatus* (see below).

Dionda episcopa punctifer (Garman), Parras roundnose minnow.—This fish was described, as *Hybognathus* (*Dionda*) *punctifer*, from material collected at Parras and in a spring near Saltillo, Coahuila, Mexico; the latter lies in the basin of the Río San Juan, a tributary of the lower Río Grande. As determined by Carl L. and Laura C. Hubbs, the Parras population is extinct. It may have represented a local form belonging to the *D. episcopa* complex. A plausible explanation for the disappearance of this fish from Parras is given above.

Lepidomeda altivelis Miller and Hubbs, Pahranagat spinedace.—This recently described species inhabited the outflow of Ash Spring and the chain of lakes in Pahranagat Valley, Nevada, into which these waters flow. The species was first collected in 1891 and became extinct between 1938 and 1959. Modification of its habitat and competition with introduced species are believed to have been responsible for its extermination (Miller and Hubbs, 1960, pp. 27–28).

Lepidomeda mollispinis pratensis Miller and Hubbs, Big Spring

spinedace.—This subspecies was endemic to a single spring-fed marsh near Panaca, Lincoln County, Nevada, in the basin of Meadow Valley Wash, a flood tributary to the Virgin River (Hubbs and Miller, 1948, pp. 98–100, map 1, no. 65). Recent agricultural modifications of the area and the introduction of exotics, especially *Gambusia a. affinis*, are held to be important factors that led to the extermination of this localized population, sometime between 1938 and 1959 (Miller and Hubbs, 1960, pp. 21–23).

Pantosteus species.—This sucker has been collected only once, in 1938, at the northern end of Spring Valley, eastern Nevada (Fig. 1). In an effort to obtain further specimens, Carl L. Hubbs and I revisited Spring Valley in 1959 and thoroughly worked the same stream where the species was collected 21 years earlier. No specimens were secured. Other waters in the valley bottom were either fishless or contained only a small minnow; mountain streams have only planted trout. Deterioration of stream flow is a plausible explanation for the extinction of this endemic sucker.

Cyprinodon radiosus Miller, Owens Valley pupfish.—This species, restricted to the northern part of Owens Valley, California, was formerly abundant in ditches, sloughs, swamps, and bog pastures that featured this part of the valley in the early 1900's. The population was then sufficiently large to serve as an effective means of mosquito control. As its habitat suffered through tapping of the water supply and drainage of the swamps, the species began to decline; introduction of exotics, particularly largemouth bass, presumably hastened its disappearance (Miller, 1948, pp. 94–95). The species has not been taken since 1939 and in all probability is now extinct.

Cyprinodon bovinus Baird and Girard, Leon Springs pupfish.—This species is known only from Leon Springs (Clark Hubbs, 1957, p. 101), about 8 miles west of Fort Stockton (Fig. 1), Pecos County, Texas. It was described from 16 specimens taken in 1851 and, to my knowledge, has not been collected since then. In 1938, Carl L. Hubbs attempted to secure material and in 1950 Howard E. Winn and I worked the spring sources and their outlets exhaustively but to no avail. Local testimony in 1950 asserted that the spring heads had been treated with rotenone ("about 4 or 5 years ago") for the purpose of eliminating the hordes of carp. The Leon Springs pupfish probably disappeared through the combined attack of habitat restriction, modification of the source springs it lived in, and the introduction of such

exotics as *Gambusia a. affinis*, *Micropterus salmoides*, and the still persistent carp.

Cyprinodon latifasciatus Garman, Parras pupfish.—This distinctive species, like *Stypodon signifer*, once inhabited a spring or springs near Parras, Coahuila, Mexico. It occurred there in 1880 and at least until 1903, when George Hochderfer obtained 9 specimens (USNM 50970). It has not been taken since and is very likely extinct. The probable causes of its extermination are given above under the account of *Stypodon signifer*.

Gambusia gaigei Hubbs, Big Bend gambusia.—This species was first discovered at Boquillas Spring, near the Río Grande, Texas, in 1928, but became extinct there by 1954. It was more recently collected at Graham Ranch Warm Springs. There, in 1954, nearly 95 per cent of the population of *Gambusia* was *G. gaigei*, the remainder *G. affinis*; in 1956, however, the proportions were reversed, so that the known population of *G. gaigei* sank to a very low level. The more widespread and aggressive mosquitofish, *G. affinis*, had probably been introduced (Clark Hubbs and Springer, 1957, p. 305). The imminent danger of extinction of the Big Bend gambusia was subsequently relieved by action of the National Park Service, which eliminated the introduced species and stocked the native one in other springs. However, on April 16, 1960, Clark Hubbs (*in litt.*) found the surviving population of *G. gaigei* to be very small since Río Grande species, including *G. affinis*, had penetrated the waters reserved for the native species, which is unable to compete successfully with them. In a last-ditch attempt to save the Big Bend gambusia, Dr. Hubbs carried back to Austin more than half of the population. It was estimated by him that fewer than 24 individuals of the species existed and that the wild population would become extinct by midsummer, 1960. It is hoped that several hundred individuals may be reared from the brood stock returned to Austin and that Big Bend National Park may successfully be restocked. The species was prematurely reported to be extinct by Matthiessen (1959, p. 271).

Gila crassicauda (Baird and Girard), thicktail chub.—This species, which reached a length of about 1 foot, formerly was common in lowland waters of the Central Valley of California (including Clear Lake and Coyote Creek, a southern tributary to San Francisco Bay[3]);

[3] The supposed occurrence of the species in Salinas River, tributary to Monterey Bay, is questionable (Clark Hubbs, 1947, p. 148).

it evidently preferred the sluggish parts of streams, sloughlike channels, and marshy or lacustrine conditions. From the 1850's to about 1880, it was sufficiently abundant to be marketed at San Francisco (Rutter, 1908, pp. 112, 117). In October, 1872, the Hassler Expedition obtained 43 specimens (MCZ 18372, 18743–746) from the Sacramento River, and Gustav Eisen collected 5 from Fresno in 1881 (USNM 30226, 107752). Midden material from an Indian mound near Oakley, Contra Costa County (close to the junction of the Sacramento and San Joaquin rivers), collected by Sherburne F. Cook, includes pharyngeal bones and teeth of the thicktail chub (W. I. Follett, letter of April 7, 1960).

Reduction of its habitat through drainage, dam building, and diversion of water for irrigation, coupled with competition from numerous exotic species, are believed to have been important factors in its impending demise. On August 29, 1926, Carl L. Hubbs and Leonard P. Schultz collected 3 hybrids between *Gila crassicauda* and *Lavinia exilicauda* (UMMZ 94166) in Putah Creek, 4 miles west of Davis, California. A hybrid between these 2 species occurred in 1872 among specimens collected by the Hassler Expedition (MCZ 35692). The thicktail chub was seldom taken after the early 1900's and, to my knowledge, only 5 specimens have been obtained since 1936: 3 from Putah Creek, 3 air miles southeast of Davis (Sacramento State Coll. Mus. No. 112) on June 26, 1936; 1 from Clear Lake, caught on May 18, 1938 (SU 37361); and another from the vicinity of Río Vista on the Sacramento River, taken on August 7, 1950 (CAS 20456). By the late 1940's the species no longer survived in Clear Lake (Murphy, 1951). This chub now is obviously on the brink of extinction, but perhaps is surviving locally. W. I. Follett made several trips since 1950 to the Río Vista region but failed to capture the species.

Gila nigrescens (Girard), Chihuahua chub.—This species, collected in 1851 from the Mimbres River north of Deming, New Mexico, is restricted to streams of interior drainage that flow into several isolated basins of northern Chihuahua, Mexico (Miller and Uyeno, MS). Its extermination from the United States has been noted by Koster (1957, p. 57), who thought its disappearance was probably due to the introduction of the longfin dace, *Agosia chrysogaster*, from the Gila River basin. However, the chub was gone when Carl L. Hubbs collected in the Mimbres on June 30, 1938, prior to the establishment of the dace. I think its disappearance is likely due to the elimination

of deep holes in the Mimbres River; a local informant told Dr. Hubbs that in the 1880's such holes (frequented elsewhere by this species) were numerous, that the stream had a more reliable and constant flow, and that he caught many 6-inch "Gila trout," the local name of this species. The terminus of the Mimbres was described in the 1850's as comprising pools or lagoons, surrounded by willow thickets, and 4 to 6 miles above it was up to 2½ feet deep and flowing at (during summer) 2½ miles per hour (Antisell, 1857, p. 176).

Gila[4] *mohavensis* (Snyder), Mohave chub.—This fish is endangered because its numbers, over almost all of its natural range in the Mohave River, California (Fig. 1), have been severely reduced by hybridization and competition with an introduced minnow, *G. orcutti* (Hubbs and Miller, 1943, 1948, p. 41). The species forms a pure and large population at only one locality in the basin, a spring-fed artificial pond, the site of a health resort, on the western side of Soda (Dry) Lake; it was abundant there on July 1, 1959. An attempt to establish this fish in other suitable but fishless waters was made in 1939 and 1940, and although the introduction was initially a success in Sentenac Canyon (San Diego County, California) the population died out there between 1957 and 1959. How long it will continue to persist in the Mohave River basin is problematical.

Lepidomeda vittata Cope, Little Colorado spinedace.—This species, endemic to the upper part of the Little Colorado River, Arizona, has been collected only 3 times since 1873—once in 1938 and twice in 1939. It belongs to a unique, small group of New World minnows, confined to the Colorado River system, that are peculiar in having spinose dorsal and pelvic rays (Miller and Hubbs, 1960). Whether the species still persists, in the face of competition with introduced species and modification of its environment, is questionable (reservoirs have been built and fish toxin used in the main river since 1939; see Hemphill, 1954). Since this statement was written, extensive efforts to collect this fish during August 1960 resulted in the capture of but a single specimen in Clear Creek, a tributary of the Little Colorado River.

Catostomus macrops Rutter, Modoc sucker.—This species was de-

[4] The reference of this species to *Gila* rather than to *Siphateles* results from unpublished studies of the comparative osteology of the genus *Gila* and its relatives by Tetuya Uyeno (Ph.D. thesis, 1960, Univ. of Mich.). He regards *Siphateles* as a synonym of *Gila*, a viewpoint with which I agree.

scribed from Rush Creek, a small tributary of Ash Creek, near Adin, Modoc County, California, in the upper basin of Pit River, a part of the Sacramento River system. Three specimens were collected there on September 1, 1898 (Rutter, 1908, pp. 120–121, fig. 1). So far as I am aware, this sucker was not taken again until August 16, 1934, when Carl L. Hubbs secured 27 specimens (UMMZ 130643) from Rush Creek about 6 miles above Adin; no additional collections have come to my attention. In response to my request for information on the status of this species, J. B. Kimsey (letter of May 4, 1960) wrote that the California Department of Fish and Game failed to take any suckers in the 3.7 mile section of lower Rush Creek that was used as a test stream from 1947 to 1951. This, however, is not the part of the stream from which the Modoc sucker has been collected. An effort should be made to determine whether this extremely localized fish still survives and, if so, to provide the means for its protection.

Chasmistes liorus Jordan, June sucker.—The status of this species, known only from Utah Lake, Utah, is not clear. Tanner (1936, p. 166) tentatively synonymized it with *Catostomus fecundus* Cope and Yarrow, but these 2 suckers, as well as *C. ardens* Jordan and Gilbert, are best regarded as valid, pending critical study of the types and all available material. The species was formerly common, as was the trout of Utah Lake. The severe drought of the mid-1930's, coupled with domestic use of the waters of Provo River (the principal source of Utah Lake), so severely reduced the sucker population of the lake that in 1935 commercial fishing was abandoned, and, according to Tanner (1936, p. 167), there was no spring spawning migration up Provo River for the first time in history. However, a few fish of this type, or possibly hybrids, were collected in this stream by Carl L. Hubbs in 1942, and an adult was captured in Utah Lake by B. Arnold (Utah Dept. of Fish and Game) on March 21, 1959. If not yet extinct, this species is certainly seriously threatened.

Chasmistes cujus Cope, cui-ui.—This species formerly spawned in the lower Truckee River, Nevada, and was abundant in deep water in the two lakes—Pyramid and Winnemucca—at the terminus of the river. During the spectacular spawning run, this large sucker provided a major source of food for the Indians and was of great importance in their tribal economy. Snyder (1917, p. 53) wrote: "The flesh of this species is highly prized by the Indians. In former times the coming of the 'cui-ui' was a great event, not only for the Pyramid Lake tribe

but also for other Piutes from far to the south, who sometimes reached the fishing grounds in such a starved condition that many were unable to survive the first feast. At present numerous little camps may be seen along the river during the spawning period. The fishes are caught in large numbers and tons of them are dried for later use. They are taken most easily when the river is roily, the fishermen hooking them with an improvised gaff which is drawn quickly through the muddy water. Knowing the 'cui-ui' habit of resting in schools in quiet water, the Indian establishes his camp accordingly, and the willows, wire fence, or hastily constructed rack are soon covered with unsalted drying fish, which attract numbers of flies and send characteristic odors a long distance down the wind."

With the development of dams, irrigation, and reclamation projects during the past half century, the lowered water level of the Truckee River and the complete desiccation of Winnemucca Lake have restricted the cui-ui to Pyramid Lake where, fortunately, the species has been able to spawn successfully along the shoreline. Unlike the native cutthroat trout (see elsewhere), this sucker is maintaining a sizable population in Pyramid Lake at the present time (1958), and thus is surviving despite the environmental disturbance wrought by man. The early life history is unknown, since specimens smaller than a foot in length have never been captured.

Empetrichthys merriami Gilbert, Ash Meadows killifish.—This and the following species of the relict genus *Empetrichthys* are confined to isolated waters of the Death Valley system in southern Nevada (Miller, 1948, pp. 99–105, pls. 10–11). *E. merriami*, rare 20 years ago, may now be extinct; it has not been taken in Ash Meadows since 1942 and, during the period from 1936 to 1942, only 22 specimens were secured by myself and others.

Empetrichthys latos Miller, Pahrump killifish.—This species was locally abundant at 3 places in Pahrump Valley in 1942. However, Ira La Rivers has written (February 2, 1960) that many changes have taken place in the valley since then and that a couple of years ago only 1 of the 3 localities was still relatively undisturbed by man's activities. Although all 3 populations were then extant, the abundance of carp and bullfrogs and the pumping dry of the spring sources and ponds render it unlikely that this killifish can survive indefinitely without protection.

Cyprinodon diabolis Wales, Devils Hole pupfish.—This extraor-

dinary fish is confined to a single cave-spring hole in Ash Meadows, Nevada. In its small population size it is nearly unique among vertebrates (matched only by the whooping crane) and is peculiar in lacking pelvic fins, in the small size attained (mature at 15–20 mm., standard length), and in its coloration and life colors. The temperature of its restricted habitat fluctuates narrowly between 91° and 93° F., and the tiny fish occur only rarely to a depth of 50 feet, although the pool is more than 150 feet deep. The total population of this species probably varies between 100 and 300 individuals; a rather accurate estimate of a total population of 160 fish, of which approximately 100 were adults representing the effective breeding population, was made recently (Miller, in press).

This species has been able to maintain itself over many thousands of years because of the isolation of its habitat in a rather remote desert area. However, in order to prevent a man-made catastrophe from eliminating the species, the Devil's Hole area (40 acres) was added to Death Valley National Monument early in 1952. Even so, a species with a home range much smaller than that of a backyard swimming pool must be considered endangered.

Cyprinodon elegans Baird and Girard, Comanche Springs pupfish.—This distinctive species was based on a series of both sexes taken in 1851 from Comanche Springs at Fort Stockton, Texas. Although the type locality of *C. bovinus* (Leon Springs) is less than 10 miles distant, the 2 species are remarkably different. *C. elegans* was common in Comanche Springs on September 15, 1938, when Carl L. Hubbs and party collected 110 specimens. Although the springs stopped flowing during the summer of 1951, after a prolonged period of drought, *Cyprinodon* still persisted in pools in the outlet ditch in April 1952 (observation by Earl S. Herald), and specimens were collected at Comanche Springs by Frank T. Knapp and class on July 30, 1952 (material at Texas A & M College). However, by October, 1956, Clark Hubbs found the springs and outlet to be completely dry, with no trace of fish life. The largest of the spring pools was about 100 by 400 feet in major dimensions and the total spring flow, in 1938, was stated to be 35 million gallons daily, which is approximately 54 second-feet, since a second foot of water is equal to about 646,000 gallons per day (Meinzer, 1927, p. 3). The discharge, in second feet, was 66 in the summer of 1899, 64 on July 26, 1904, and 44 on August 21, 1919 (Meinzer, 1927, p. 41).

Although the Comanche Springs population of *Cyprinodon elegans* appears to have become extinct, the species still persists in Phantom Lake and its outlet near Toyahvale, Texas.

Characodon lateralis Günther.—This species was recorded from Parras, Coahuila, before the turn of the century, but has not been taken there since (Hubbs and Turner, 1939, p. 57). Like *Stypodon signifer* and *Cyprinodon latifasciatus,* it has probably been exterminated from Coahuila, for reasons given under the account of *Stypodon.* The only member of an endemic Mexican family otherwise living farther to the south, this fish still persists in the headwaters of the Río Mezquital around Durango City, Durango.

Archoplites interruptus (Girard), Sacramento perch.—This, the only native sunfish west of the Rocky Mountains (Miller, 1959, p. 199, figs. 8–9), is an interesting relict endemic to the Central Valley and neighboring coastal streams of California. It was very abundant in early days, inhabiting sloughs and sluggish channels as well as lakes.[5] Its numbers have been greatly reduced, presumably by the establishment of exotic species and changing ecological conditions, so that it has become scarce over its native range except in a few isolated localities. Its spawning habits are unique for the family since no nest is built and the eggs are unguarded (Murphy, 1948). Jordan and Gilbert (1894) wrote of the species in Clear Lake: "Formerly very common, but now becoming scarcer as its spawning grounds are devastated by the carp. . . . The destruction of this valuable fish is one of the most unfortunate results of the ill-advised introduction of the carp into California waters." Failure of the adults to guard the eggs was not serious in aboriginal times but has subsequently made the species vulnerable to predation by such introduced species as the bluegill. Although endangered in its natural habitat, the species has become successfully established elsewhere, for example in Walker Lake, Nevada.

Gasterosteus aculeatus williamsoni Girard, unarmored threespine stickleback.—This freshwater stickleback was based on 8 specimens collected in 1853 in "Williamson's Pass," California, which is in the headwaters of Santa Clara River (Fig. 1), Los Angeles County (Miller, 1961). It has apparently always been restricted in the Santa

[5] In 1849, for example, it was abundant and grew to be 15 to 20 inches long in lakes in the San Joaquin and Tulare valleys (Harris, 1960, p. 106, as "black perch").

Clara to its upper part and has, at times, been very difficult to find there. On the other hand it was "abundant everywhere" in 1912–13 in the then flowing streams of the Los Angeles Plain, just to the south (Culver and Hubbs, 1917). It still occurred in the Los Angeles River as late as 1929 (USNM 94343), but disappeared there within the next decade; it was probably during this same period that it vanished from the Santa Ana River, for the last record there of which I am aware is for 1923 (CAS 18558), and none was found during careful investigation along the river in the late 1930's. By 1939, this stickleback occurred on the Los Angeles Plain apparently only in the San Gabriel River system near Whittier, where it was last taken in April 1942 (UMMZ 139009).

Changing water conditions, especially the disappearance of former perennial flows (see p. 371), and competition with introduced fishes have evidently brought about the extinction or near extinction of this fish over that part of its range where it once was most abundant. *Gambusia affinis affinis* has very likely been the principal exotic responsible for the disappearance of the stickleback; the mosquitofish was introduced and widely established in California in 1922 (Dill, 1944, p. 162), and was common in the Los Angeles area by 1930. Whether *G. a. williamsoni* still survives on the Los Angeles Plain is questionable; it was still present in the upper part of Santa Clara River in 1951 and probably persists also in the Mohave River at Victorville (where it has been introduced, and was last collected in 1955).

DEPLETION AND SPECIES REPLACEMENT

The Arizona native trout, which I have tentatively referred to *Salmo gilae* (Miller, 1950, p. 34), once inhabited suitable tributaries of Salt River, Gila River (in New Mexico as well as Arizona), and the headwaters of the Little Colorado River (Fig. 1). It is the only trout indigenous to Arizona.[6] Testimony from old-timers and records

[6] I have examined specimens of the trout recorded by Jordan and Evermann (1896, p. 496) as *Salmo clarki pleuriticus* from the Little Colorado River and identify them as the Arizona native trout. The occurrence of the latter in the Little Colorado drainage is the result of introduction by way of an 1897 canal diversion (from a tributary of White River), or by transplanting activities of early stockmen, or both (letter from Jack E. Hemphill, November 10, 1960). This fish is well portrayed in color on the cover of the pamphlet by Mulch and Gamble (1954).

kept by F. M. Chamberlain (see p. 373) have shown how the range of *S. gilae* has dwindled since around the turn of the century (Miller, 1950, pp. 18–20, 27–29). Additional information on its former distribution and abundance in Oak Creek, south of Flagstaff, was obtained from Stanley Sykes in Flagstaff on May 25, 1950. He came to Arizona from Kansas in 1886, and first went down into Oak Creek Canyon in 1888, by a very rough trail. Native trout, as long as 16 inches, were then abundant as far downstream as the small falls (now just above the first highway crossing north of Sedona), and were easily caught. Before 1900, however, Sykes observed that introduced rainbow trout had already started to displace the native trout through competition and hybridization (see also Miller, 1950, p. 28), and it is doubtful whether a remnant of the pure stock still persists anywhere in the Verde River drainage. Dan A. Purtyman, Superintendent of the Page Springs Fish Hatchery on Oak Creek, testified that he helped stock the first rainbow trout in the creek when he was a boy (shortly before 1900). The last native trout he saw in Oak Creek was in 1915 or thereabouts; these trout were yellowish and spotted and lacked the "rainbow" band and the "cutthroat" mark.

In his letter of June 30, 1939, to Carl L. Hubbs, E. C. Becker, of Springerville, related information obtained from his father, Gustav Becker, who came to Arizona in 1876. This testimony is concerned with the native trout—"yellow bellies," as they were called—of the White Mountains, in both the headwaters of the Little Colorado and Salt rivers, and with the early history of trout stocking in the Little Colorado River. Such documentation is difficult to find in print and much valuable information has disappeared with the passing of old-timers. No exotic species were planted between 1876 and 1917, for the streams were apparently always stocked to capacity from natural reproduction. From 1898 to 1916, E. C. Becker stated that the native trout "were so plentiful that it was no trick for a boy to catch 100 in a few hours or 200 in a full afternoon." Because of ancient taboos against eating fish, the trout were not eaten by the Apache Indians and so survived until the white man began to exploit them. In 1917, brook trout (*Salvelinus fontinalis*) were brought from Holbrook and planted above Greer. A short time later, the rainbow trout (*Salmo gairdneri*) was introduced. When the South Fork Hatchery was built 10 miles from Springerville, in 1921, rainbow and "Wyoming natives" (*S. clarki lewisi*) "were distributed to practically all the accessible

streams." Since then the Loch Leven or brown trout (*S. trutta*) has been added. Whether there are still uncontaminated stocks of native Arizona trout in the headwaters of the Little Colorado River I am not sure, but a sample collected by E. C. Becker at about 11,000 feet (near the summit of Mt. Ord) in 1938 represents the original form (UMMZ 157653).

A native cutthroat trout, *Salmo clarki* Richardson, was once common in Pine Valley and Grass Valley, southwestern Utah, at the head of Santa Clara River. It may have inhabited upper tributaries of the North Fork of the Virgin River, above Zion National Park, according to Vere Beckstrom whom I contacted in 1950 at the Pine Valley store. In 1907, he caught 350 native trout in Pine Valley in one day. I also talked to M. E. Bracken of Central, Utah, then 93 years old. He came to St. George in 1861 and to Pine Valley in 1863, when he first saw the trout. Most individuals did not exceed 12 inches and were "better tasting than rainbow or brown." The "mountain trout" did not come far down the streams, not much beyond the junction of the "Middle Fork and Left Fork" in Pine Valley. Mr. Bracken believed that trout were planted in the region shortly after 1900. Native trout still persisted in the headwaters of Pine Valley as late as 1934, when Arthur Paxman and V. M. Tanner collected 7 specimens (deposited at Brigham Young University). All informants were in accord, in 1950, that the only native stock still persisting is confined to the upper part of Main Canyon Creek in Grass Valley. Kumen Gardner, owner of Gardner Ranch near the mouth of Main Canyon, informed me that the creek was planted with rainbow trout during the period from 1915 to 1920, but not since then. It is now necessary to hike several miles up above the ranch to Reservoir Canyon to obtain the native trout, as most of the fish taken near the ranch show characters that indicate hybridization and backcrossing between the rainbow and native cutthroat (observations in 1950 and 1959; material at Michigan). In 1910, Mr. Gardner said that he easily caught 100 native trout a day.

Depletion and extermination of the cutthroat trout fishery in Pyramid Lake, Nevada, have been described at length (Sumner, 1940; Trelease, 1949), and numerous other instances of the disappearance of native trouts could be cited (e.g., see Pratt, 1937).

The Colorado squawfish or "salmon," as it is locally known, is one of the world's largest minnows and was an important source of food

for the aborigines that lived along the lower Colorado and Gila rivers (Miller, 1955). It probably approached a maximum length of 6 feet and a weight of nearly 100 pounds, although record weights over the past 35 years are not known to have exceeded 40–50 pounds. At one time this predatory, pikelike fish was common in the river channels throughout the Colorado River basin, wherever there was sufficient depth and current. Until about 1911, the species was so abundant in the lower Colorado that individuals got into the irrigation ditches and were pitchforked out onto the banks by the hundreds for use as fertilizer. Vast numbers of "salmon," bonytails, and humpback suckers perished in this fashion or died when they were unable to re-enter the river from the irrigated lands (testimony of Walter K. Bowker, Jr., Imperial Valley Irrigation District, March 23, 1950). In the early days the Indians used to tie 2 sticks together, with netting between, and dip "salmon" out of the river. From 1911 to 1920, "salmon" were numerous in the Gila River near Dome, according to R. C. Richardson, Bureau of Reclamation employee and long-time fisherman. Earlier, between about 1845 and 1885, the species occurred more widely in the Gila River basin in Arizona (Miller, 1955), and it may still persist in the deep canyons of Salt River where 2 young were caught by R. R. Miller and party on May 18, 1950 (at mouth of Cibecue Creek, Gila County; UMMZ 162779). A sharp decline in abundance was noticed in the lower Colorado in the 1930–35 period, during the construction and completion of Hoover Dam and the great 1934 drought, at the height of which the river was reduced to a shallow trickle at Yuma (Dill, 1944). Specimens of *Ptychocheilus* weighing 6 to 34 pounds (Wallis, 1951, p. 90) were caught along the lower Colorado in the 1930's and 1940's but records of the species after 1949 are scarce. In the Gila River basin the last adult was caught in 1937 (in Salt River, above Roosevelt Dam), according to T. T. Frazier, informed local resident, who reported that the species had been fairly common there in 1906.

Changing ecological conditions, competition, and direct predation have no doubt strongly influenced the depletion of the Colorado squawfish and bonytail, so that both species are now nearly extirpated from the lower river. The humpback sucker, however, appears to be holding its own in the man-made reservoirs. Extensive recent sampling in the lower Colorado by the California Department of Fish and Game, in connection with an evaluation of the introduced

threadfin shad (*Dorosoma petenense*), has failed to reveal native fishes other than *Xyrauchen texanus* (letter of January 6, 1958, from J. B. Kimsey to Carl L. Hubbs). Both *Ptychocheilus lucius* and *Gila robusta elegans* may still be caught in sections of the Colorado River above Grand Canyon, but the series of dams now under construction there may well mean extermination for these fishes in the not too distant future.

The Conchos pupfish, *Cyprinodon eximius* Girard, was described from Chihuahua City, Chihuahua, Mexico, in 1859. On May 29, 1903, S. E. Meek collected it in the independent drainage of the Río Sauz at Sauz, about 30 miles northward from Chihuahua City. Testimony obtained by Clark Hubbs during the summer of 1954 indicates that the Río Sauz went dry in 1947 and that "there is no living water anywhere in the valley" (letter of July 6, 1954, from Clark Hubbs to Carl L. Hubbs). Whatever local attributes this population may have developed during its isolation from the main range of the species will have to be determined solely from the preserved material.

Arivaca Creek, a small spring-fed stream that rises just above Arivaca, southern Arizona (Fig. 1), was originally fishless, according to Fred C. Noon (contacted on April 15, 1950, at Oro Blanco Ranch). It was stocked by the Arizona State Health Department with *Gambusia* during a malaria outbreak about 1936. Thorough examination in 1950 of the main part of the creek (about 175 yards long), above and below the road crossing, revealed only the Gila topminnow (*Poeciliopsis occidentalis*), which may have been the fish introduced as "*Gambusia*" about 1936, reportedly from the vicinity of Tucson. It was stated that catfish and bass had been planted on the flat above Arivaca, but these species were unknown in the creek. The native topminnow was again found to be common there on April 12, 1957, when I secured a live stock for experimental work. On March 30, 1959, however, when the stream was revisited to replenish our live material, *Poeciliopsis* had been completely replaced by the exotic mosquitofish, *G. affinis affinis*. How and when the latter species gained entry to Arivaca Creek is not known, but *P. occidentalis* was replaced by the more competitive alien in a rather short time—apparently in less than 2 years. Charles H. Lowe, Jr., of the University of Arizona, visited the creek in June, 1959, expressly to check my finding and also was unable to locate a single specimen of *Poeciliopsis*. The introduction of *G. affinis* in other parts of the Southwest has led to the reduc-

tion or elimination of the less competitive native fishes (see p. 389), even including cyprinids (personal observations in California, and observations by Clark Hubbs in Texas—personal communication, 1959). *P. occidentalis* is now so scarce throughout Arizona that it is definitely threatened with extinction there.

Factors in Depletion and Extinction

In a very perceptive unpublished report[7] resulting from 2 months of field work in Arizona in the spring of 1904, the late F. M. Chamberlain (an assistant with the old U. S. Bureau of Fisheries) outlined the major causes of the depletion and extinction of fish life in Arizona. His material is incorporated into the following summary, which includes a consideration of additional factors that later became operative in further changing the native fauna of the Southwest. Many of the factors discussed below were effective at a much earlier time in producing faunal change in eastern North America (e.g., see Barnickol and Starrett, 1951, p. 323; Lachner, 1956; Trautman, 1957, pp. 13–24).

Destruction of vegetation.—Over much of the Southwest, large expanses were originally covered by a luxuriant growth of grasses and other succulent herbage which, during the rainy season, reached a height of 2 feet or more (Leopold, 1951). As the dry season advanced, the vegetation died down but formed a protective mulch, and its roots were remarkably effective in binding the soil. Such a cover acts like a sponge in retaining rainfall and hence is a potent defense against erosion. Not only were valley floors covered in part by dense sacatón grass but there were extensive ciénegas (wet meadows) near their centers, and elsewhere the water table was often within a few feet of the surface (Thornber, 1910, p. 334). Consequently, there were many more permanent streams than now, and large floods were rare (Antevs, 1952).

With the introduction and establishment of livestock, the vegetation was not only eaten progressively shorter but it was severely trampled to expose the soil over much of the area within a radius of daily movement from water (Gregory, 1950, pp. 44–45). Such denudation by herds became particularly noticeable after 1875 (Antevs, 1952) and led to increased floods and severe erosion. Unbelievably

[7] Deposited in the Division of Fishes, U. S. National Museum, Washington, D. C.

destructive floods may originate in a region of depleted soil and plant cover whereas adjacent, well-vegetated areas may at the same time receive no damaging runoff (Bailey, 1941, p. 245). The catastrophic nature of stream erosion after ecological disturbance by man has been dramatically described and illustrated for Kanab Creek, Arizona (Gregory, 1950, pp. 174–175, fig. 113). Bryan (1925, p. 342) stated that in only 10 years the channel of the San Pedro River of southern Arizona was incised from its mouth for 125 miles upstream.

Destruction of the climax grassland by excessive grazing and trampling has, since about 1890, allowed the rapid spread of the aggressive mesquite tree beyond the bottom lands to which it was formerly confined. The serious effects of this invasion are recognized by those concerned with the use and conservation of vegetative cover, land, and water. The increase and spread of mesquite has been accompanied by a rise in the population of certain small rodents which further disseminate the mesquite; thus a vicious circle has set in. Rodent pressure alone may prevent the revegetation of deteriorated grasslands that are overburdened with mesquites (Glendening and Paulsen, 1955, pp. 45–47).

The conspicuous arroyos of our semiarid regions, so prominent in Arizona and New Mexico, were largely cut between about 1880 and 1910. Their streams are mostly ephemeral, their channels have flat bottoms and vertical walls, and they range in size to 100 feet deep, many hundreds of feet wide, and 140 miles long (Antevs, 1952). That these erosive gashes were brought on by excessive numbers of livestock has been fully demonstrated by Thornber (1910) and others (see Thornthwaite et al, 1942, pp. 120–122).

Cutting of timber in the forested headwater areas for use in mines, for fuel, for house construction, and in clearing land also promoted rapid runoff, and often a lowering of the water table, and resulted in damaging erosion from floods. Removal of protective vegetation led not only to depletion of perennial streams and lowering of the water table but also to the destruction of habitats for fish life in the surviving waters. The filling in of deep pools by sand and silt has eliminated species that habitually seek and require such places for survival, and the water has been rendered unfit for respiration when completely saturated with silt (Ellis, 1936; Wallen, 1951). Reduction or elimination of aquatic plants and increasing water temperatures have also profoundly affected the survival of aquatic organisms.

Irrigation and dams.—Consumption of water is the chief way in which irrigation operations affect fish life. Once diverted from the river it is expended on the land and lost by evaporation. Fishes may be carried out into the canals and ditches at the point of diversion and later perish when the water is cut off or as the habitat becomes unsuitable. Dams prevent upstream migration and in years of low water all fish below them may be killed as the stream bed becomes dry. The prevention of upstream movement may particularly affect large fishes, such as the Colorado squawfish, that develop in the lower courses of rivers but spawn in tributaries. The greatly altered habitat produced by impoundments may prove to be wholly unsuited to the native species—especially when, as so frequently happens, they are placed into competition with introduced species.

Mining operations.—The sediments from concentrating mills rapidly fill up river channels and destroy fish habitats in much the same way as do floods. Thus streams become barren for considerable distances below the point of entry of such wastes. Cyanide and other poisons resulting from ore processing also may denude a stream of all life if such chemicals are permitted free access to surface waters. Although chemical pollution is very destructive, its effects have generally been local in the Southwest and have not seriously threatened the native fish fauna. It has had more serious consequences outside of the area under discussion (Ellis, 1914, pp. 128–129; Sumner and Smith, 1940). Industrial pollution has risen in importance with increasing population trends. Familiarity with powder in mining operations has also led to the use of dynamite as a means of obtaining fish—a destructive practice since only a small proportion of the animals killed can usually be recovered. Such a fishing method, if widely used, may lead to streams nearly barren of fish life.

Depletion of ground water.—Pumping of water and the deep trenching of the valley floors has gradually lowered the water table in the Southwest. Springs and ciénegas went dry, streams ceased to flow or diminished in size, and wells had to be drilled to greater depths. Continuing demands for increased water supply following the population explosion since World War II have brought about an even more drastic lowering of the water table. For example, in 1950, one of the few remaining perennial flows of the Santa Cruz River went dry near San Xavier Mission for the first time in recorded his-

tory. Even when exceptionally heavy runoff occurs, the expected additional recharge of the water table by downward percolation now fails to be effective—probably because of shallow penetration and subsequent evaporation (Smith, 1940, p. 41).

Introduction of exotics.—With the establishment of the U. S. Fish Commission in 1872 the march of exotics began with the introduction of the carp. Today the number of native and introduced species inhabiting certain southwestern states shows that the indigenous fauna of any state does not outnumber the planted kinds by more than 3 to 1, generally only about 2 to 1; in Arizona, however, there are more exotics than there are natives. The following figures are derived from the references cited plus the author's manuscript checklists: Colorado, 54 native and 33 exotic species (Beckman, 1952); New Mexico, 61 native and 22 introduced kinds (Koster, 1957); Arizona, 28 native, 37 stocked fishes; Utah, 26 native, 24 planted species; Nevada, 41 native and 21 exotic kinds (La Rivers and Trelease, 1952); and California, 67 native fresh-water and anadromous species and 32 introduced species (Shapovalov, Dill, and Cordone, 1959).

The period of intensive introductions occurred chiefly between 1930 and 1950, along with the construction of major dams and diversions and the marked increase in human population. Most of these alien species—numbering approximately 36—came from eastern United States, in large part as intentional plants of game fishes. Only 8 exotic species are known to have become established in the West prior to 1930.

Many of the established aliens have affected the native species either directly—through predation, competition, and hybridization (Hubbs and Miller, 1953, and earlier references cited)—or indirectly, by altering the habitat (as carp have done). In the Mohave River of eastern California the one native fish has been almost wiped out through competition and hybridization with a better-adapted exotic species (Hubbs and Miller, 1943, 1948, and subsequent unpublished studies). The western mosquitofish, *Gambusia a. affinis*, has ousted native species and subspecies through competition and predation, so that some indigenous forms are now threatened with extermination. The complete replacement of *Poeciliopsis* by *Gambusia* at Arivaca Creek, Arizona, possibly in less than 2 years, has been described above. Ellis (1914, p. 129) attributed the scarcity of the yellowfin

trout of Twin Lakes, Colorado, to the introduction of a deep-water competitor, the lake trout (*Salvelinus namaycush*)—a species that has raised havoc with native trouts in other lakes of the West.

Chemical treatment.—The use of toxic chemicals, such as rotenone and toxaphene, for the control or eradication of fish populations may have serious consequences for the native species. Such a management tool is being employed more and more widely in the control of "rough fish"; without prior determination of its harmful effects, this practice may needlessly exterminate localized species or relict populations (see above and Koster, 1957: 106). Its relatively indiscriminate use in streams has already reduced certain native fishes to dangerously low levels or has seemingly brought about local extinction (Clark Hubbs, *in litt.*, 1960). Conservationists should make a determined effort to prevent the decimation of aquatic biota in this way, if necessary through the enactment of protective legislation.

Changing climate.—This factor has been cited by some as the initial cause of the recent excessive erosion in the arid Southwest (see on the contrary, Bailey, 1935, and Antevs, 1952). Tree-ring and other records clearly indicate that periods of arid and of wet conditions are recurrent and are a basic character of climate (Sears, 1957). However, the severe erosion of the past century is invariably associated with man's direct or indirect disturbance of the environment. Had the native vegetation been left alone the arroyo cutting that commenced in the 1880's would probably not have materialized.

Summary

During the past 100 years, the aquatic habitats and the fish faunas of the American Southwest have undergone marked changes. Six or 7 species have become extinct and at least 13 others have been either locally exterminated or are so endangered that they too may soon vanish. These 19 or 20 species constitute almost 20 per cent of the known aboriginal fishes of Western North America (north of Mexico).

Reduced flow of surface waters has shrunk the ranges of many species and the distribution of others has been curtailed by the construction of barrier dams. Drastic reduction in ground-water levels has also eliminated or restricted the habitats of aquatic organisms. The establishment of some 36 species of exotic fishes has brought about replacement as well as reduction of the native forms through

competition, predation, and hybridization. Because of the depauperate nature of the fauna and the circumstance that the distribution of many of the endemic species has been restricted (some are recent, others old, relicts), they probably lack the defense mechanisms that characterize species of more saturated faunas; thus they are rather easy prey for the typically more aggressive introduced fishes.

There is little evidence that the aborigines had much effect on the original fauna. The changes began soon after colonization by the white man, around the middle of the nineteenth century. During the period from 1880 to 1915, when most of the deep trenching (arroyo cutting) of the valley floors took place in the arid Southwest, once permanent streams withered through erosion from accelerated runoff, drainage of ciénegas, and lowering of the water table. The major modifications that have taken place over much of the region are illustrated by the changes that certain rivers and valleys have undergone. The deterioration of the fish faunas is indicated by repeated collections, some of which span a century, at several stations in Arizona. Testimony of old-timers indicates the general trend toward depletion of native stocks.

Interference by man with delicate and complex ecological balances has had dire consequences in many parts of the world. Perhaps nowhere else in North America has the upset of natural conditions been more strikingly reflected by biotic change than in the arid Southwest, particularly in southern Arizona. Overwhelming evidence indicates that modern man, rather than climatic change, has been the chief agent in producing the observed changes. Removal of vegetation by overgrazing and forest cutting has been the most important single cause of erosion. The deterioration of the native fish faunas can also be plausibly attributed to construction of dams, water diversions, pollution, mining operations, use of toxic chemicals, depletion of ground water, and the introduction of alien species.

LITERATURE CITED

Antevs, Ernst. 1952. Arroyo-Cutting and Filling. Jour. Geol., 60(4): 375–385.

Antisell, Thomas. 1857. Geological Report. *In*: Pacific Railroad Expl. and Surv., 7(2): 1–204, pls. 1–14, 2 maps.

Bailey, Reed W. 1935. Epicycles of Erosion in the Valleys of the Colorado Plateau Province. Jour. Geol., 43(4): 337–355, figs. 1–11.

—— 1941. Land Erosion—Normal and Accelerated—in the Semiarid West. Trans. Am. Geophys. Union, pt. 2: 240–250.

Barnickol, Paul G., and William C. Starrett. 1951. Commercial and Sport Fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Bull. Ill. Nat. Hist. Surv., 25(5): 267–350, figs. 1–15, col. frontis.

Beckman, William C. 1952. Guide to the Fishes of Colorado. Univ. Colo. Mus., Leaflet 11: 1–110, figs. 1–13, illus.

Beland, Richard D. 1953a. The Effect of Channelization on the Fishery of the Lower Colorado River. Calif. Fish and Game, 39(1): 137–139, fig. 1.

—— 1953b. The Occurrence of Two Additional Centrarchids in the Lower Colorado River, California. *Ibid.*, 39(1): 149–151.

Bryan, Kirk. 1925. Date of Channel Trenching (Arroyo Cutting) in the Arid Southwest. Science, 62: 338–344.

Colton, Harold S. 1937. Some Notes on the Original Condition of the Little Colorado River: A Side Light on the Problems of Erosion. Mus. Notes, Mus. N. Ariz., 10(6): 17–20, figs. 1–3.

Cope, E. D., and H. C. Yarrow. 1875. Report upon the Collections of Fishes Made in Portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, During the Years 1871, 1872, 1873, and 1874. Rept. Geog. and Geol. Expl. and Surv. W. 100th Merid. (Wheeler Survey), 5: 635–703, pls. 26–32.

Culver, George B., and Carl L. Hubbs. 1917. The Fishes of the Santa Ana System of Streams in Southern California. Lorquinia, 1(11): 82–83.

Dill, William A. 1944. The Fishery of the Lower Colorado River. Calif. Fish and Game, 30(3): 109–211, figs. 45–82.

Dipeso, Charles C. 1951. The Babocomari Village Site on the Babocomari River, Southeastern Arizona. Amerind Foundation, No. 5: i–xii, 1–248, figs. 1–49, pls. 1–76.

Ellis, Max M. 1914. Fishes of Colorado. Univ. Colo. Stud., 11(1): 1–136, 1 fig., 3 maps, pls. 1–12.

—— 1936. Erosion Silt as a Factor in Aquatic Environments. Ecol., 17(1): 29–42, fig. 1.

Emory, W. H. 1848. Notes of a Military Reconnoissance, from Fort Leavenworth, in Missouri, to San Diego, in California, Including Parts of the Arkansas, Del Norte, and Gila Rivers. 30th Cong., 1st Sess., Senate Exec. No. 7: 1–126, illus.

Fenneman, Nevin M. 1931. Physiography of Western United States. McGraw-Hill Book Co., i–xiii, 1–534, figs. 1–173, pl. 1.

Gehlbach, Frederick E., and Robert Rush Miller. 1961. Fishes from Archeological Sites in Northern New Mexico. Southwestern Nat.

Gilbert, Charles H., and Norman B. Scofield. 1898. Notes on a Collection of Fishes from the Colorado Basin in Arizona. Proc. U. S. Nat. Mus., 20: 487–499, pls. 36–39.

Glendening, George E., and Harold A. Paulsen, Jr. 1955. Reproduction and Establishment of Velvet Mesquite as Related to Invasion of Semidesert Grasslands. U. S. Dept. Agr. Tech. Bull. 1127: 1–50, figs. 1–24.

Glidden, E. H. 1941. Occurrence of *Elops affinis* in the Colorado River. Calif. Fish and Game, 27(4): 272–273.

Gregory, Herbert E. 1950. Geology and Geography of the Zion Park Region, Utah and Arizona. U. S. Geol. Surv., Prof. Pap. 220: i–vi, 1–200, figs. 1–133, pls. 1–5.

Harris, Benjamin Butler. 1960. The Gila Trail/The Texas Argonauts and the California Gold Rush. Univ. Oklahoma Press, i–xv, 1–175, illus.

Hemphill, Jack E. 1954. Toxaphene as a Fish Toxin. Prog. Fish-Cult., 16(1): 41–42.

Henderson, Junius, and Wilfred William Robbins. 1913. Climate and Evidence of Climatic Changes. *In:* The Physiography of the Rio Grande Valley, New Mexico, in Relation to Pueblo Culture. Smith. Inst. Bur. Am. Ethnol., Bull. 54: 41–70, figs. 1–2.

Hubbs, Carl L. 1953. *Eleotris picta* Added to the Fish Fauna of California. Calif. Fish and Game, 39(1): 69–76, figs. 1–2.

—— 1954. Establishment of a Forage Fish, the Red Shiner (*Notropis lutrensis*), in the Lower Colorado River System. *Ibid.*, 40(3): 287–294, figs. 1–3.

—— and Robert R. Miller. 1943. Mass Hybridization between Two Genera of Cyprinid Fishes in the Mohave Desert, California. PMASAL,[8] 28 (1942): 343–378, figs. 1–2, pls. 1–4.

—— and ——. 1948. Correlation between Fish Distribution and Hydrographic History in the Desert Basins of Western United States. *In:* The Great Basin, with Emphasis on Glacial and Postglacial Times. Bull. Univ. Utah, 38(20): 17–166, figs. 10–29, 1 map.

—— and Robert Rush Miller. 1953. Hybridization in Nature between the Fish Genera *Catostomus* and *Xyrauchen*. PMASAL, 38(1952): 207–233, figs. 1–3, pls. 1–4.

—— and C. L. Turner. 1939. Studies of the Fishes of the Order Cyprinodontes. XVI. A Revision of the Goodeidae. Misc. Publ. Mus. Zool. Univ. Mich., 42: 1–80, pls. 1–4.

Hubbs, Clark. 1947. Mixture of Marine and Fresh-Water Fishes in the Lower Salinas River, California. Copeia, 1947(2): 147–149.

—— 1957. Distributional Patterns of Texas Fresh-Water Fishes. Southwestern Nat., 2(2–3): 89–104, figs. 1–2.

—— and Victor G. Springer. 1957. A Revision of the *Gambusia nobilis* Species Group, with Descriptions of Three New Species, and Notes on Their Variation, Ecology, and Evolution. Texas Jour. Sci., 9(3): 279–327, figs. 1–15.

Jordan, David Starr, and Barton Warren Evermann. 1896. The Fishes of North and Middle America. Part I. Bull. U. S. Nat. Mus., 47: i-lx, 1–1240.

Jordan, David S., and Charles H. Gilbert. 1894. List of the Fishes Inhabiting Clear Lake, California. Bull. U. S. Fish. Comm., 14 (1895): 139–140.

Kimsey, J. B., Robert H. Hagy, and George W. McCammon. 1957. Progress Report on the Mississippi Threadfin Shad, *Dorosoma petenensis atchafalayae*, in the Colorado River for 1956. Calif. Dept. Fish and Game,

[8] PMASAL = Papers Mich. Acad. Sci., Arts, and Letters.

Inland Fish. Branch, Admin. Rept. No. 57-23: 1–48 (mimeo.). [cited from Shapovalov et al., 1959]

Koster, William J. 1957. Guide to the Fishes of New Mexico. Univ. New Mexico Press, i–vii, 1–116, illus.

Lachner, Ernest A. 1956. The Changing Fish Fauna of the Upper Ohio Basin. *In*: Man and the Waters of the Upper Ohio Basin. Pymatuning Lab. Field Biol., Spec. Publ. No. 1: 64–78.

La Rivers, Ira, and T. J. Trelease. 1952. An Annotated Check List of the Fishes of Nevada. Calif. Fish and Game, 38(1): 113–123.

Lee, Willis T. 1907. Water Resources of the Rio Grande Valley in New Mexico. U. S. Geol. Surv. Water-Supply and Irrigation Pap. 188: 1–59, pls. 1–10.

Leopold, Luna B. 1951. Vegetation of Southwestern Watersheds in the Nineteenth Century. Geog. Rev., 41: 295–316, figs. 1–4.

Matthiessen, Peter. 1959. Wildlife in America. The Viking Press, N. Y., 304 pp., illus.

McGlashan, H. D. 1930. Surface Water Supply of Pacific Slope Basins in Southern California, 1894–1927. U. S. Geol. Surv. Water-Supply Pap. 636E: i–vi, 169–219.

Meinzer, Oscar E. 1927. Large Springs in the United States. U. S. Geol. Surv. Water-Supply Pap. 557: i–vii, 1–94, figs. 1–23, pls. 1–17.

Mendenhall, Walter C. 1908. Ground Waters and Irrigation Enterprises in the Foothill Belt, Southern California. U. S. Geol. Surv. Water-Supply Pap. 219: 1–180, figs. 1–16, pls. 1–9.

Miller, Robert Rush. 1948. The Cyprinodont Fishes of the Death Valley System of Eastern California and Southwestern Nevada. Misc. Publ. Mus. Zool. Univ. Mich., 68: 1–155, figs. 1–5, maps 1–3, pls. 1–15.

—— 1950. Notes on the Cutthroat and Rainbow Trouts with the Description of a New Species from the Gila River, New Mexico. Occ. Pap. Mus. Zool. Univ. Mich., 529: 1–42, map 1, pl. 1.

—— 1952. Bait Fishes of the Lower Colorado River from Lake Mead, Nevada, to Yuma, Arizona, with a Key for Their Identification. Calif. Fish and Game, 38(1): 7–42, figs. 1–32.

—— 1954. A Drainage Map of Arizona. Syst. Zool., 3(2): 80–81.

—— 1955. Fish Remains from Archaeological Sites in the Lower Colorado River Basin, Arizona. PMASAL, 40(1954): 125–136, fig. 1, pls. 1–5.

—— 1959. Origin and Affinities of the Freshwater Fish Fauna of Western North America. *In*: Zoogeography. Amer. Assoc. Adv. Sci., Publ. 51 (1958): 187–222, figs. 1–19.

—— 1961. The Type Locality of *Gasterosteus aculeatus williamsoni* and Its Significance in the Taxonomy of Californian Sticklebacks. Copeia, 1960 (4).

—— In press. Speciation Rates in Some Freshwater Fishes of Western North America. *In*: Vertebrate Speciation. Univ. Texas Press.

—— and Carl L. Hubbs. 1960. The Spiny-Rayed Cyprinid Fishes (Plagopterini) of the Colorado River System. Misc. Publ. Mus. Zool. Univ. Mich., 115: 1–39, figs. 1–2, pls. 1–3.

—— and Teruya Uyeno. MS. Classification of the Cyprinid Fishes of the Genus *Gila* in Southwestern United States and Mexico.

Mulch, Ernest E., and William C. Gamble. 1954. Game Fishes of Arizona. Ariz. Game and Fish Dept., 1954: 1–19, 5 figs., 8 col. pls., col. frontis.

Murphy, Garth I. 1948. A Contribution to the Life History of the Sacramento Perch (*Archoplites interruptus*) in Clear Lake, Lake County, California. Calif. Fish and Game, 34(3): 93–100, figs. 26–29.

—— 1951. The Fishery of Clear Lake, Lake County, California. *Ibid.*, 37(4): 439–484, figs. 175–179.

Olmstead, Frank H. 1919. A Report on Flood Control of the Gila River in Graham County, Arizona. 65th Cong., 3d Sess., Senate Doc. No. 436: 1–94, many maps and figs., pls. 1–32.

Parke, John G. 1857. General Report. *In*: Pacific Railroad Expl. and Surv., 7(1): 1–42, pls. 1–8.

Pratt, Harold. 1937. Population Studies of the Trout of the Gunnison River. Univ. Colo. Stud., 24(2): 107–116, figs. 1–2.

Ross, Clyde P. 1923. The Lower Gila Region, Arizona. U. S. Geol. Surv., Water-Supply Pap. 498: i–xiv, 1–237, figs. 1–16, pls. 1–23.

Rutter, Cloudsley. 1908. The Fishes of the Sacramento-San Joaquin Basin, with a Study of Their Distribution and Variation. Bull. U. S. Bur. Fish., 27(1907): 103–152, figs. 1–4, pl. 6.

Schwalen, Harold C. 1942. Rainfall and Runoff in the Upper Santa Cruz River Drainage Basin. Univ. Ariz. Agr. Expt. Sta., Tech. Bull. 95: 421–472, figs. 1–10, pls. 1–7, frontis.

Sears, Paul B. 1957. The Ecology of Man. Condon Lectures, Oregon State Sys. Higher Ed., Eugene, Ore., 1957: 1–61, figs. 1–15.

Shapovalov, Leo, William A. Dill, and Almo J. Cordone. 1959. A Revised Check List of the Freshwater and Anadromous Fishes of California. Calif. Fish and Game, 45(3): 159–180.

Sitgreaves, L. 1853. Report of an Expedition down the Zuni and Colorado Rivers. 32d Cong., 2d Sess., Sen. Ex. Doc. 59: 1–29, 1 map, illus.

Smith, G. E. P. 1940. The Groundwater Supply of the Eloy District in Pinal County, Arizona. Univ. Ariz. Agr. Expt. Sta., Tech. Bull. 87: 1–42, figs. 1–7, pls. 1–3.

Snyder, John Otterbein. 1915. Notes on a Collection of Fishes Made by Dr. Edgar A. Mearns from Rivers Tributary to the Gulf of California. Proc. U. S. Nat. Mus., 49: 573–586, 1 fig., pls. 76–77.

—— 1917. The Fishes of the Lahontan System of Nevada and Northeastern California. Bull. U. S. Bur. Fish., 35(1915–16): 33–86, figs. 1–9, pls. 3–5.

St. Amant, J. A. 1959. Striped Bass Introduced into the Colorado River. Calif. Fish and Game, 45(4): 353.

Sumner, Francis H. 1940. The Decline of the Pyramid Lake Fishery. Trans. Am. Fish. Soc., 69(1939): 216–224, figs. 1–2.

—— and Osgood, R. Smith. 1940. Hydraulic Mining and Debris Dams in Relation to Fish Life in the American and Yuba Rivers of California. Calif. Fish and Game, 26(1): 2-22, figs. 1–10.

Tanner, Vasco M. 1936. A Study of the Fishes of Utah. Utah Acad. Sci., Arts and Letters, 13: 155–184, pls. 1–3.

Thornber, J. J. 1910. The Grazing Ranges of Arizona. Ariz. Agr. Expt. Sta., Bull. 65: 335–338.

Thornthwaite, C. W., C. F. S. Sharpe, and Earl F. Dosch. 1942. Climate and Accelerated Erosion in the Arid and Semi-Arid Southwest with Special Reference to the Polacca Wash Drainage Basin, Arizona. U. S. Dept. Agr., Tech. Bull. 808: 1–134, figs. 1–57.

Trautman, Milton B. 1957. The Fishes of Ohio. Ohio State Univ. Press, Columbus, xvii + 683 pp., 172 maps, 11 col. pls., 172 figs.

Trelease, Thomas J. 1949. What Lies Ahead for Pyramid Lake. Nev. Hunting and Fishing, 1(2): 8–10, 23, 29–32, illus.

Wallen, I. Eugene. 1951. The Direct Effect of Turbidity on Fishes. Bull. Okla. Agr. and Mech. Coll., Biol. Ser. 2, 48(2): 1–27, figs. 1–5.

Wallis, Orthello L. 1951. The Status of the Fish Fauna of the Lake Mead National Recreational Area, Arizona-Nevada. Trans. Am. Fish. Soc., 80(1950): 84–92, fig. 1.

Whipple, A. W. 1856. Report on the Topographical Features and Character of the Country. *In*: Pacific Railroad Expl. and Surv., 3(2): 1–77, illus.

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THE NORTH AMERICAN SCIOMYZIDAE RELATED TO *PHERBELLIA FUSCIPES* (MACQUART) (DIPTERA ACALYPTRATAE)

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The genera of the subfamily Sciomyzinae found in North America may be separated as follows:

1 (2). Fore tibiae with 2 preapical bristles.
2 (3). Arista with long black rays; face not tuberculate... Sciomyza Fallén
3 (2). Arista densely short white plumose; face tuberculate above Oidematops Cresson
4 (1). Fore tibiae with 1 preapical bristle.
5 (6). Anal vein not attaining wing margin; basal cells small; fore coxae with 3–5 bristles.....Colobaea Zetterstedt
6 (5). Anal vein attaining wing margin; basal cells large; fore coxae rarely with as many as 3 bristles.
7 (8). Propleural bristles fine and thin; center of propleura, nearly entire mesopleura and sternopleura, and center of pteropleura with fine longish hairs; fore coxae without bristles.....Atrichomelina Cresson
8 (7). Propleural bristle strong; 1 or more of the above pleural regions without fine hairs; fore coxae with at least 1 bristle.
9 (10). Predominantly shining black species; cheeks linear; frons wholly shining.....Pteromicra Lioy
10 (9). Species of yellow, brown, or gray color, never shining black; cheeks at least moderately wide; frons partly or wholly opaque. Pherbellia Robineau-Desvoidy

Pherbellia is likely a composite group. About a decade of genera have been proposed for various segregates, but the characters upon which they are based seem trivial and in some cases intergrading. Until an exhaustive study of the male postabdomen can be completed, it seems best to recognize but a single genus.

A key to one group of *Pherbellia*, those in which the shining interfrontal stripe extends two-thirds or more of the distance from the anterior ocellus to the frontal margin, including the generitype *P. schoenherri* (Fallén), has been presented.[1] The remainder of the genus at

[1] Steyskal, G. C., 1949. New Diptera from Michigan (Stratiomyidae, Sarcophagidae, Sciomyzidae) PMASAL, 33: 173–180.

this time seems best divisible on the extent of the setation of the mesopleura. Three groups are distinguishable: (*a*) one in which setulae are present over a considerable part of the mesopleura; (*b*) one in which the mesopleura are wholly bare; and (*c*) one in which a narrow row of setulae is found along the posterior margin of the mesopleura.

This latter group, which I am treating here, may be considered as typified by the European species *Pherbellia fuscipes* (Macquart). Seven very similar species of this group have been found in North America. As will be seen below, little more than characters of the male postabdomen seems to be available to distinguish the species. These characters, however, when the postabdomen is properly macerated and extended, I have found fully reliable. Female specimens of most of the species are consequently indeterminable.

The postabdomen of *Pherbellia* species, when removed and macerated as outlined in my revision of *Dictya*,[2] remains largely withdrawn into the epandrium. A careful tug at the aedeagus with a fine forceps will bring the parts into full and comparable view as shown in the figures.

Five Palaearctic species may be assigned to this group: *Pherbellia fuscipes* (Macquart); *P. albocostata* (Fallén); *P. appendiculata* (Hendel), comb. nov.; *P. austera* (Meigen), comb. nov.; and *P. griseola* (Fallén). *P. albocostata* and *P. griseola* have been previously recorded from North America; I have confirmed their presence here by comparison of male postabdomens (v.i.). *P. fuscipes* has been recorded as common in North America, but I have seen no material from this continent which agrees in characters of the male postabdomen with Palaearctic specimens. Five other species, here described as new, do occur in North America. The other two Palaearctic species, *P. austera* and *P. appendiculata*, apparently do not occur in North America.

KEY TO NORTH AMERICAN SPECIES RELATED TO *PHERBELLIA FUSCIPES* (MACQ.)

1 (2). Wings with pale yellowish costal border; veins Sc, R_1, and R_{2+3} yellow, remaining veins brown; arista short plumose; pteropleura with several hairs, but with no outstanding bristles; hind coxae bare above at

[2] Steyskal, G. C., 1954. The American Species of the Genus Dictya Meigen (Diptera, Sciomyzidae). Entom. Soc. Am., Ann., 47: 511–539.

apex; female fore tibiae and tarsi black; male postabdomen as in Fig. 2 ..... *P. albocostata* (Fallén)

2 (1). All wing veins brown; wings uniformly subhyaline or at least without paler costal border, the cross veins often seamed with brown; pteropleura with several hairs and also 2 or 3 distinctly stronger bristles.

3 (4). Hind coxae with a few hairs on dorsal apex; aristal hairs long (Fig. 3a; male postabdomen as in Fig. 3) ..... *P. seticoxa*, sp. nov.

4 (3). Hind coxae bare on dorsal apex; aristal hairs moderate to long.

5 (6). Cerci (male) approximately as long as posterior surstyli; profile of epandrium pentagonal, ventral margin angularly projecting (Fig. 1); aristal hairs relatively short (Fig. 1a) ..... *P. griseola* (Fallén)

6 (5). Cerci (male) much shorter than posterior surstyli; profile of epandrium quadrate.

7 (8). Posterior surstyli thick, cylindrical, abruptly tapering to sharp mucro at tip; anterior surstyli apically with sharply pointed anterior process and longer blunt posterior process (Fig. 7) ..... *P. oregona*, sp. nov.

8 (7). Posterior surstyli more gradually tapering or slender; anterior surstyli more or less trilobate apically.

9 (10). Posterior surstyli with broad base rapidly narrowed to slender, only slightly tapering process; anterior wing of phallobase with oval, backwardly projecting lobe (Fig. 4); aristal hairs rather short (Fig. 4a) *P. quadrata*, sp. nov.

10 (9). Posterior surstyli gradually tapering; anterior wing of phallobase otherwise.

11 (12). Anterior wing of phallobase with two sharply pointed, backwardly directed teeth; posterior surstyli straight, with small spatulate tip (Fig. 5) ..... *P. footei*, sp. nov.

12 (11). Anterior wing of phallobase with backwardly projecting digitate lobe; posterior surstyli sharply pointed and curved inwards *P. idahoensis*, sp. nov.

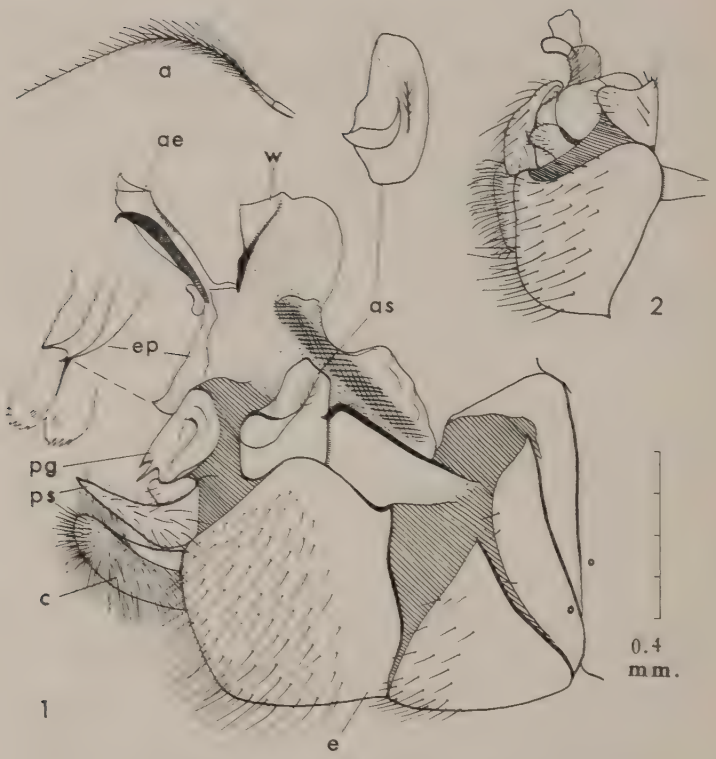
The shape of the anterior surstylus, the pair of processes which may be postgonites (Fig. 1, pg), and the median structures posterior to the aedeagus (epiphallus, ep) should be noted, since they also exhibit good specific differences.

Pherbellia albocostata (Fallén)

(Fig. 2)

Sciomyza albocostata Fallén, 1820, Sciomyz. Sueciae: 12; Aldrich, 1905, Smithsonian Misc. Coll. 46: 577.
Melina albocostata (Fallén) Cresson, 1920, Am. Entom. Soc., Trans., 46: 45; Melander, 1920, Entom. Soc. Am., Ann., 13: 314.
Pherbellia albocostata (Fallén) Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 249.

North American specimens of this species have been checked against material from Europe (Denmark; Austria) and found con-



Details of *Pherbellia* Species, Male

Fig. 1. *Pherbellia grisescens* (Fallen). Black Sturgeon Lake, Ont.: Sinistral profile of extended postabdomen; arista.

Fig. 2. *P. silvaticostata* (Fallen). Sylvan Lake, S. D.: Sinistral profile of extended postabdomen.

Legend: a—arista; ae—aedeagus; as—anterior surstylus (with separate perpendicular view); c—cerci; e—epandrium; pg—postgonite; ps—posterior surstylus; w—anterior wing of phallobase.

Note: Legend and scale are same for all figures.

specific. It is somewhat different from the other species herein treated in the characters cited in the key and in those of the postabdomen. I have seen material from Maine (Mt. Katahdin), New Hampshire (Mt. Washington), South Dakota (Lead; Spearfish; Sylvan Lake), Colorado ("Colorado"), and British Columbia (Fort Nelson; Kaslo; Selkirk Mts.). These localities include some cited by Aldrich, Cresson, and Melander. Johnson also cites Vermont, Massachusetts, and Connecticut.

Pherbellia footei Steyskal, sp. nov.

(Fig. 5)

Male. Length of wing, 5.2 mm. Wings subhyaline, with brown seams on crossveins *ta* and *tp*. Hind coxae bare above. Aristal hairs moderately short, approximately as shown for *P. quadrata* in Fig. 1a. Postabdomen with epandrium quadrate in profile; cerci much shorter than posterior surstyli, which are straight, strongly tapering, and with small spatulate lobe at tip; anterior surstyli trilobate apically, the anterior lobe narrow and turned sidewise, posterior base of surstylus with deep pocket; anterior wings of phallobase with pair of posteriorly directed teeth; epiphallus with channel ending in sharp point followed by oval, leaflike lobe.

Female. Not recognized.

Holotype (male), Bancroft, Caribou Co., Idaho, August 3, 1958 (B. A. Foote); paratype (male), Bear Lake, Bear Lake Co., Idaho, July 19, 1959 (B. A. Foote); both in University of Idaho collections.

This species is related to *Pherbellia idahoensis* and *P. quadrata*, differing from both in details of the postabdomen and from the former in apparently smaller size and shorter aristal hairs.

Pherbellia fusca (Cresson), comb. nov.

Melina fusca Cresson, 1920, Am. Entom. Soc., Trans., 46: 43.
M. spadix Cresson, 1920, Am. Entom. Soc., Trans., 46: 42 (in key).

Cresson cited the unique type as being a female specimen from University, North Dakota, June, 1896 (R. P. Currie) [U.S.N.M.]. I have examined a specimen in the U. S. National Museum labeled as holotype of the Cresson species. University, North Dakota, probably refers to the University of North Dakota, situated 2 miles from the center of the town of Grand Forks. Since the specimen is a female it is at present unidentifiable. The aristal hairs are short and the hind coxae are bare above.

Pherbellia griseola (Fallén)

(Fig. 1)

Sciomyza griseola Fallén, 1820, Sciomyz. Sueciae: 14.
Melina griseola (Fallén) Melander, 1920, Entom. Soc. Am., Ann., 13: 314.

Postabdomens of *Pherbellia* Species, Male

Fig. 5. *Pherbellia footei*, sp. nov., paratype, Bear Lake, Idaho.
Fig. 6. *P. idahoensis*, sp. nov., paratype, Pullman, Wash.; with perpendicular view of anterior surstylus of paratype from Klamath Lake, Ore.

Pherbellia griseola (Fallén) Steyskal, 1954, Entom. Soc. Wash., Proc., 56: 55. Misdetermination.

Melander cited this species from Montana and Wyoming. I have examined a male specimen from Three Forks, Montana, August 1, 1918, belonging to the Washington State College collection and collected and determined by Melander. I have also seen material from New York (Albion), Michigan (Grosse Ile; Munising; Gratiot, Lapeer, Osceola, and Tuscola counties); Idaho (Donnelly, Valley Co.; Latah Co.), Washington (Coupeville), Utah (Hole-in-Rock Canyon, Uintah Co.), Ontario (Black Sturgeon Lake), and Quebec (Hudson Heights), which compares well with a specimen from the Netherlands. My determination of material from Alaska is erroneous and refers to a quite different species.

In view of the presence in the western United States of at least three other very closely similar forms, Melander's Wyoming record should be checked. I have not been able to separate females of this species from those of *P. footei, P. idahoensis, P. oregona*, and *P. quadrata* with any certainty, and males have been separable only by examination of macerated postabdomens, wherein the outstanding characters are those cited in the key.

The wing length in available male specimens varies from 4.4 to 5.0 mm., the species thus being smaller than most specimens of related species.

Pherbellia idahoensis Steyskal, sp. nov.

(Fig. 6)

Male. Length of wing, 5.3 to 6.4 mm. Wings subhyaline, with brown seams on *ta* and *tp*. Hind coxae bare above. Arista with rather long hairs, approximately as shown for *P. seticoxa* in Fig. 3a. Postabdomen with epandrium quadrate in profile; cerci much shorter than posterior surstyli, which are curved mesad, strongly tapering, sharply pointed, and with distinct basal tooth alongside cerci; anterior surstyli trilobate apically, the anterior lobe broader than the posterior lobe, the median lobe an elevation on the mesal margin of the posterior lobe; posterior base of surstylus with deep pocket; anterior wings of phallobase with posteriorly directed digitate process and semicircular apical lobe; epiphallus with channel bounded by strongly declivitous walls and ending in a declivity beyond which is a thin rounded flange.

Female. Not recognized.

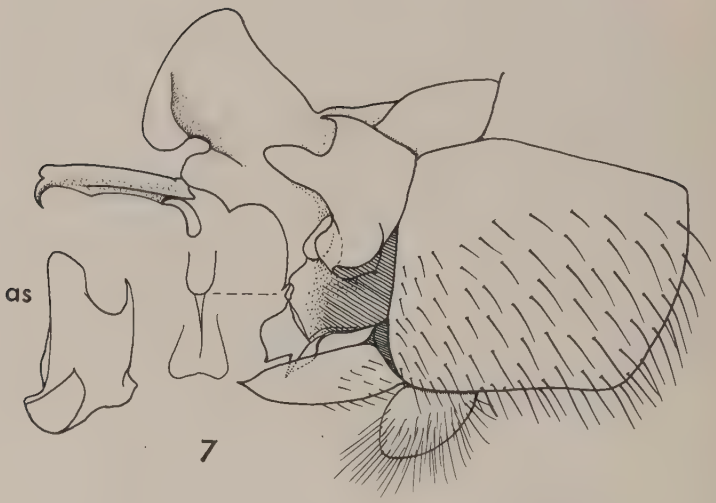
Holotype (male) and one male paratype, Moscow, Latah Co., Idaho, August 11, 1958 (B. A. Foote); male paratypes, Pullman, Whitman Co., Wash. (det. *Melina fuscipes* by Melander); Klamath Falls, Klamath Co., Ore., July 3, 1954 (Joe Schuh). All specimens have been returned to the University of Idaho.

This species is a member of the closely related complex including *P. footei* and *P. quadrata*, from which it differs in postabdominal details and in having longer aristal hairs.

Pherbellia oregona Steyskal, sp. nov.

(Fig. 7)

Male. Wings subhyaline, with brown seams on *ta* and *tp*. Hind coxae bare above. Postabdomen with epandrium quadrate in profile; cerci much shorter



Postabdomen of *Pherbellia* Species, Male

Fig. 7. *Pherbellia oregona*, sp. nov., holotype, Forest Grove, Ore.

than posterior surstyli, which are thick, cylindrical, and abruptly tapering to sharply mucronate tip; anterior surstyli bilobate apically, the anterior lobe sharply pointed, the posterior lobe much broader and blunt; anterior wings of phallobase with short roundish lobe projecting posteriorly; epiphallus with shallow, round-ended channel followed by cuneiform foliate process.

Female. Unknown.

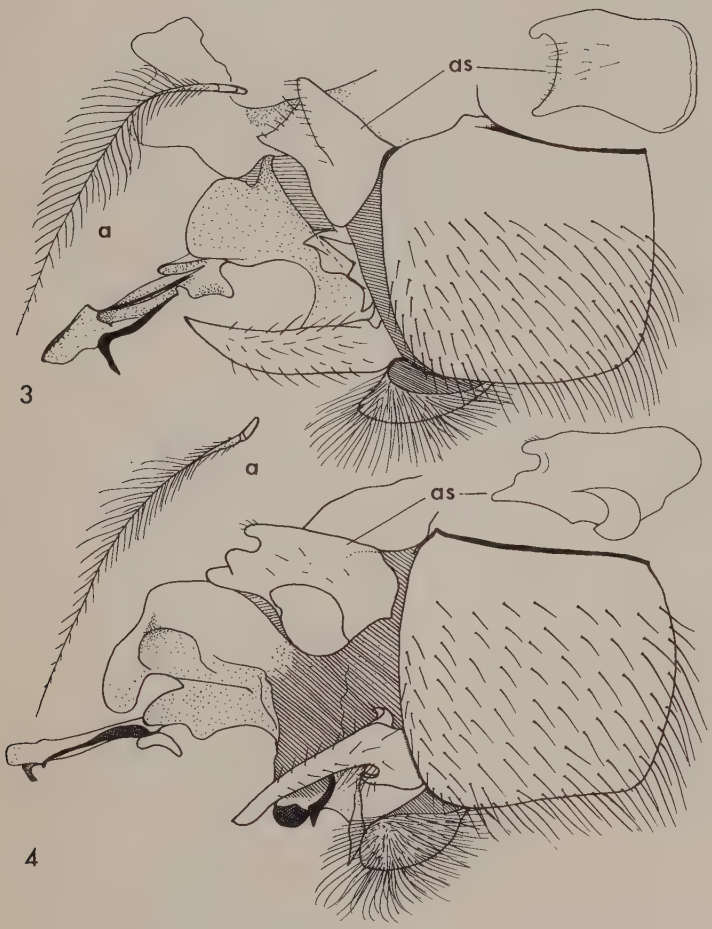
Holotype (male), Forest Grove, Washington Co., Ore., May 8, 1938, in mechanical trap; returned to University of Idaho.

This species is apparently most closely related to the eastern *P. seticoxa*, differing therefrom in details of the postabdomen and in lacking hairs on upper side of hind coxae.

Pherbellia quadrata Steyskal, sp. nov.

(Fig. 4)

Male. Length of wing, 4.6 to 5.4 mm. Wings subhyaline, with brown seams on *ta* and *tp*. Hind coxae bare above. Aristal hairs moderately short. Postabdomen with epandrium quadrate in profile; cerci much shorter than the slender, straight, only slightly tapering posterior surstyli, which have broad bases somewhat curved upwards mesally and tips abruptly hollowed out on mesal side; anterior surstyli trilobate, posterior base with deep pocket; anterior wings of phallobase



Postabdomens and Aristae of *Pherbellia* Species, Male

Fig. 3. *Pherbellia seticoxa*, sp. nov., holotype, Grosse Ile, Mich. N.B.: The basal structures between the surstyli are not fully extended and the arista is shown partly overlying the anterior wing of phallobase.

Fig. 4. *P. quadrata*, sp. nov., holotype, Alpena County, Mich.

with tongue-like lobe directed posteriorly; epiphallus with channel ending in sharp point followed by foliate lobe, much as shown for *P. footei* in Fig. 3.

Female. Not definitely recognized.

Holotype (male), Alpena Co., Mich., July 30, 1953 (G. Steyskal); paratypes (male), Deerfield Twp., Lapeer Co., Michigan, May 30, 1952 (G. Steyskal); Albion, Orleans Co., New York, August 6, 1952 (G. Steyskal); Fargo, N. Dak., June 13, 1918 (J. M. Aldrich); Bear Lake, Bear Lake Co., Idaho, July 19, 1959 (B. A. Foote); Copeland, Blaine Co., Idaho, June 1, 1959 (B. A. Foote). Holotype and paratypes in my collection, paratypes in University of Idaho collection and U. S. National Museum.

This species seems most closely related to *P. idahoensis*, differing therefrom in smaller size, shorter aristal hairs, and postabdominal details.

Pherbellia seticoxa Steyskal, sp. nov.

(Fig. 3)

Male. Length of wing, 4.5 to 6.2 mm. (average of 18 specimens, 5.55 mm.). Wings subhyaline, with brown seams on *ta* and *tp* and often with broad yellowish costal border. Hind coxae with several hairs at apex on upper side. Aristal hairs rather long. Postabdomen with epandrium quadrate in profile; cerci much shorter than the posterior surstyli, which are stout, cylindrical on basal two-thirds and strongly tapering and curved mesad with sharp tip in apical one-third; anterior surstyli squarish, without pocket at base, with posterior apex forming acute straight process and anterior apex forming an inwardly curved process; anterior wings of phallobase at some distance from base of aedeagus, with backwardly directed broadly triangular lobe; epiphallus with narrow channel whose walls increase in height posteriorly and end like the heel of a slipper, without terminal foliate lobe.

Female. Length of wing, 6.0 to 7.0 mm. (average of eight specimens, 6.48 mm.). Similar to male except for sexual characters.

Holotype (male) and allotype, Grosse Ile, Wayne Co., Michigan, April 21, 1954 (G. Steyskal); paratypes (male): same locality, July 5, 1948, August 23, 1952, August 9, 1953, April 10, 1955; Detroit, Michigan, August 9, 1930; Deerfield Twp., Lapeer Co., Michigan, May 30, 1952; Macomb Co., Michigan, May 28, 1949; Ann Arbor, Washtenaw Co., Michigan, September 15, 1935 (all G. Steyskal); Midland Co., Michigan, August 21, 1943, May 26, 1945, July 14, 1947, May 16 and 21, June 16, 1948; Cherry Co., Nebraska, August 5, 1948 (all R. R. Dreisbach); paratypes (female): Grosse Ile, Michigan, August 17, 1952; Deerfield Twp., Lapeer Co., Michigan, May 30, 1952; Brant, Saginaw Co., Michigan, May 30, 1953; Albion, Orleans Co., New York, August 6, 1952 (all G. Steyskal); Gratiot Co., Michigan, June 2, 1948; Manistee Co., Michigan, September 5, 1938 (both R. R. Dreisbach). Holotype, allotype, and paratypes in my collection, paratypes in collection of R. R. Dreisbach.

This species is somewhat different from the other species treated here, and like *P. albocostata*, stands somewhat alone; it is, however, probably most closely related to *P. oregona*, which lacks the hairs on upper side of hind coxae and differs in several respects in postabdominal characters.

I have previously determined material from many sources as "*Pherbellia fuscipes*" or "*Melina fuscipes*," the following states and provinces being represented in the records: New York, Michigan, Indiana, Illinois, Wisconsin, Iowa, North Dakota, South Dakota, Colorado, Idaho, California, Washington, Alberta, Quebec. Until this material can be reviewed, it must be presumed that the records actually refer to any of the species herein treated or possibly additional undescribed species.

I wish especially to express my gratitude to Clifford O. Berg and Benjamin A. Foote, without whose interest in obtaining exact determinations for the insects whose biology they are studying this paper might not have been written.